PREY PREFERENCES OF SPECIALIZED JUMPING SPIDERS (ARANEAE: SALTICIDAE)

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ABSTRACT

I studied prey preferences of two groups of specialized jumping spiders (Salticidae), ant-eating ('myrmicophagic') species and spider-eating ('araneophagic') species, in the laboratory. Spiders and ants have in common being unusual and dangerous prey for a salticid. Ten salticid species, four species of *Portia* (*P. africana, P. fimbriata*, *P. labiata* and *P. schultzi*) which specialize at catching other species of spiders (araneophagic species) and six myrmicophagic species (*Chalcotropis* sp., *Habrocestum pulex*, *Siler* sp., *Telamonia masinloc*, and two new species of euophryines in a new genus) were studied. Each of these specialized salticid species, whether araneophagic or myrmicophagic, uses prey-specific capture behaviour against its unusual prey and also shows pronounced preferences for these prey (ants or spiders, depending on the species). The capture behaviour of the four species of *Portia* was known prior to the present study, but the description of capture behaviour of the six ant-eating salticids and the data on preferences of all species are new in this study.

Although all myrmicophagic and all araneophagic salticid species tested resemble each other by having prey-specific capture behaviour against ants and spiders, respectively, details of the predatory behaviour used against ants vary among the species, and the same is true for behaviour used against spiders.

All *Portia* species studied are known to have different prey-specific capture behaviour for use against spiders and insects. Also, they are all shown in the present study to have distinctive preferences for web-building spiders over insects as prey. However, the capture behaviour of *P. fimbriata* from Queensland is also known to differ depending on whether the prey is a web-building spider or a cursorial salticid spider: a specialized behaviour ('cryptic stalking') is used by Queensland *P. fimbriata*, but not by other *Portia*, for catching other salticids. In the present study, Queensland *P. fimbriata* is known also to prefer salticid spiders not only to insects but also to web-building spiders. In contrast, the other *Portia* species (*P. africana*, *P. labiata* and *P. schultzi*) studied prefer web-building spiders to salticid spiders as prey. This study suggests that, in specialized

salticids, the trend is: when a species has a special capture behaviour for a particular type of prey, it also shows a preference for that type of prey.

Portia shows intersexual variation in preference. In all *Portia* species studied, both the males and the females behave similarly during capture sequences against spiders (*i.e.*, use the same prey-specific capture behaviour). Also, both the males and the females of *Portia* are shown in the present study to have similar preferences for taxonomic categories of prey. However, there are intersexual differences in the size of prey preferred: males prefer smaller prey, and females prefer larger prey. Factors affecting intersexual differences in prey-size preference are discussed.

A study of *P. labiata* from Los Banos in the Philippines illustrates how prey-specific capture behaviour and prey preference may interrelate at a more fine-grain level. In nature, the diet of the Los Banos *Portia* includes *Scytodes*, an unusually dangerous prey spider. *Scytodes* is a genus of spiders with an unique predatory behaviour: these spiders spit a sticky gum from their fangs onto prey, and onto predators. I investigated interactions between *Scytodes* and four species of web-invading salticids, including *P. fimbriata* from Queensland, *P. labiata* from the Philippines and *P. labiata* from Sri Lanka. Los Banos *P. labiata*, but neither Queensland *P. fimbriata* nor Sri Lanka *P. labiata*, uses a *Scytodes*-specific capture behaviour, and also it prefers *Scytodes* as prey.

A brooding *Scytodes*, compared to a non-brooding *Scytodes*, is a safer prey for a *Portia* because the brooding *Scytodes* carries her eggs in her fangs, effectively blocking the spitting weapons. As an apparent refinement of its predatory strategy, Los Banos *P. labiata* distinctively prefers brooding *Scytodes* over non-brooding ones.

Optimal foraging theory is considered in a discussion of the factors that may have been important in the evolution of prey preferences.

SECTION I

INTRODUCTION

CHAPTER 1

Introduction

Predators are often envisaged as lying on a continuum from relatively specialized to relatively generalized, but it is important to recognize that these terms can refer to a number of different characteristics of the predator. This thesis is a step toward understanding the different ways in which jumping spiders (Salticidae) may be specialized as predators by addressing questions relating to the predator's capture behaviour and prey preference. These questions are different from questions about the predator's diet.

In relation to diet, predators are more or less stenophagous if they include only a narrow range of prey types (one or a few) in their diets and more or less euryphagous if they include a wide range of prey types in their diets. Preference may contribute to dietary specialization, but is different from diet itself (Morse, 1971, 1980; Fox & Morrow, 1981).

For example, a stenophagous predator may or may not have evolved prey-specific ('specialized') capture behaviour for use against the few types of prey in its diet. Also, a predator that is euryphagous in diet might be either 'specialized' or 'generalized' in prey-capture behaviour. That is, an euryphagous predator does not necessarily use generalized capture behaviour against all of the numerous types of prey on which it normally feeds; instead, it may be 'versatile' (Curio, 1976): it might use a conditional predatory strategy consisting of a repertoire of disparate prey-specific capture behaviours, each for a different type of prey in its broad diet. Therefore, a versatile predator may be highly specialized in capture behaviour, yet relatively euryphagous in diet.

Prey preference is yet another way in which a predator may be specialized, and it is distinct from both diet and prey-specific capture behaviour. That is, preference, which implies an ability to distinguish between different types of prey and to choose to take one rather than the other, cannot be inferred simply from knowing the animal's diet in nature or from knowing that the animal has

prey-specific capture behaviour.

Specialized diets (Morse, 1971; 1980; Fox & Morrow, 1981; Nentwig, 1986) and specialized (prey-specific) capture behaviour (Curio, 1976; Edwards *et al.*, 1974; Jackson, 1992a; Jackson & Blest, 1982a; Jackson & Hallas, 1986a) have been studied extensively in predators, but prey preference behaviour of specialized predators has received comparatively little attention (Jackson & van Olphen, 1991; 1992). The aim of this thesis is to study the prey preferences of specialized jumping spiders (Salticidae).

The Salticidae, a large family of spiders (Prószyński, 1971; Coddington & Levi, 1990) with unique, complex eyes and acute vision (Land, 1969a, b, 1974, 1985; Forster, 1982a; Blest *et al.*, 1990), may be a group in which selective foraging is especially likely: prior to contact, salticids can potentially discriminate between different types of prey (Jackson & Blest, 1982b). The typical prey of salticids are soft-bodied, more-or-less safe insects such as flies, and acute vision probably enables salticids to avoid contacting potentially dangerous prey such as ants and spiders. However, a minority of salticids feed routinely on the potentially dangerous prey (ants and spiders) avoided by most other salticids (Jackson, 1992a; Richman & Jackson, 1992).

Ten species of salticids (from 4 genera, *Brettus*, *Cyrba*, *Gelotia* and *Portia*), all from the subfamily Spartaeinae (Wanless, 1984), are known not only to prey on spiders but also to practise vibratory aggressive mimicry in the other spiders' webs (Jackson, 1992a). This is the most extreme specialization on spiders as prey known and the term 'araneophagic salticids' is restricted to these species. Each of these araneophagic species also preys on insects (either in or out of webs), and the Queensland *Portia fimbriata* also preys frequently on other salticids.

The most extensively studied araneophagic salticids are from the genus *Portia*, and in these species aggressive mimicry is combined with pronounced behavioral complexity. *Portia* has a large repertoire of vibratory signals (Jackson & Wilcox, 1993a) made by manipulating, plucking and slapping the silk with one or any combination of its legs and palps, all of which can be moved in different ways. *Portia* also makes signals by flicking its abdomen up and down, and

abdominal movements can be combined with all of the appendage movements.

The web-building spider, *Portia*'s intended victim, has acute abilities to detect and discriminate between vibratory signals transmitted over the silk in its web, but how the spider interprets these web-borne vibrations varies considerably between species and also with the sex, age, previous experience and feeding state of the spider (Witt, 1975; Jackson, 1986a; Masters *et al.*, 1986). Yet *Portia* has been observed using aggressive mimicry to catch many kinds of web-building spiders, within a range from about one tenth to twice *Portia*'s size (Jackson & Blest, 1982b; Jackson & Hallas, 1986a).

However, there is important variation among the species, and even populations of single species, of *Portia*. The most pronounced example of interpopulation difference in predatory behaviour concerns the Queensland population of *P. fimbriata*, which differs from all other *Portia* studied by having special methods for catching cursorial salticids belonging to other genera. *P. fimbriata*'s habitat in Queensland is unique among those studied in having an especially high abundance of cursorial salticids (Jackson & Hallas, 1986a) and, apparently, the Queensland *P. fimbriata*'s predatory behaviour is specially adapted to this locally abundant prey type (Jackson, 1992b).

Along with spiders, ants are potentially dangerous prey for salticids. This is because ants come equipped with strong mandibles, poisonous stings and formic acid (Eisner, 1970; Blum, 1981). Also being social insects, ants tend to be present in large numbers and can mount communal attacks on predators and prey (Wilson, 1971). All of these factors tend to present formidable challenges to most cursorial spiders (Nentwig, 1986). However, in most terrestrial environments, and especially in the tropics (where salticids appear to be the dominant spider family: Bristowe, 1941), ants are the dominant arthropods in the size range of the prey normally taken by salticids (Hölldobler & Wilson, 1990). For a salticid that overcomes the ant's defence, a rich food resource becomes available.

The araneophagic and myrmicophagic salticids can be called 'specialized' predators because their diets include ants and spiders, these being special prey that are not available for other related predators. Also, they are specialized

predators because they use specialized (*i.e.*, prey-specific) capture behaviour against these unusual and dangerous prey. However, my objective was to investigate a different kind of potential specialization - prey preference.

For establishing what prey araneophagic and myrmicophagic salticids prefer, I use the methods developed earlier for studies of myrmicophagic salticids (Jackson & van Olphen, 1991, 1992), but with modifications that allow for more efficient testing and modifications were needed when testing araneophagic salticids. Also, for the first time, I use models, in addition to living prey, to test for preferences; this allows for ruling out prey motility as a factor affecting preference. Study animals are four species of *Portia*, araneophagic salticids, and six species of myrmicophagic salticids that have not been studied previously for prey preference or prey-specific capture behaviour.

This thesis is also the first study of the influence of prey size on the preferences of specialized salticids, and it is the first consideration of how salticid males' and females' prey preferences compare.

Consideration is also given to the influence of adaptive trade-offs on the evolution of behaviour and the question of why specialized salticids have evolved their particular prey preferences. Factors related to safety and factors related to metabolic needs are highlighted, and discussed in the context of optimal foraging theory.

Seven questions about prey preferences of araneophagic and myrmicophagic salticids are addressed:

1) Do the species with prey-specific capture behaviour for catching dangerous prey (*i.e.*, ants and spiders) prefer these dangerous prey?

2) Do these species prefer certain sizes of prey?

3) Do males and females of these species prefer the same prey?

4) Does hunger level affect prey preference of these species?

5) For these species, is prey movement an essential recognition cue?

6) Do these species fine tune preferences in a way that reduces risk?

7) What evolutionary factors might have influenced these species' preferences?

The chapters in this thesis are presented in six sections. Each chapter, except for the first and last, in this thesis is written as a separate paper in the format of the journal to which it will be, or has been, submitted, and is designed to stand independently. Since the chapters are structured to stand on their own, some repetition is inevitable.

There is only one chapter (the present chapter, **Chapter 1**) in **Section I**. In this chapter, I describe my objective in this thesis, address the questions, and clarify the layout of the thesis.

In **Section II**, I examine in two chapters (**Chapter 2** & **3**) the prey preferences of myrmicophagic salticids. In **Chapter 2**, I look at *Habrocestum pulex*, a North American ant-eating salticid spider. Although there have been prior studies of the behaviour of *H. pulex*, this is the first detailed study of this species' prey-capture techniques and prey preferences. In **Chapter 3**, I look at prey-capture behaviour and prey preferences of five never-before-studied ant-eating salticid species from the Philippines. These studies suggest a hypothesis which is supported by the studies in **Section III**: in predators that have evolved prey-specific capture behaviour for use against unusual and dangerous prey, there has also been a tendency for pronounced prey preferences for these unusual and dangerous prey to evolve.

In **Section III**, which contains two chapters (**Chapter 4** & **5**), I examine prey preferences of araneophagic salticids. In **Chapter 4**, I look at the prey preferences of a salticid-eating *Portia*, *P. fimbriata* from Queensland. In **Chapter 5**, I look at the prey preferences of *Portia* that do not feed routinely on salticids, *P. africana* and *P. schultzi* from Kenya and *P. labiata* from Sri Lanka. In this chapter, I compare prey preferences among the *Portia* species, and provide more evidence related to the hypothesis proposed in **Section I**. **Chapters 4** and **5** reveal a distinctive behaviour of preferring spiders over insects as prey in all species of *Portia* studied, and a preference for salticids over other spiders uniquely in Queensland *P. fimbriata*, which is also the only population of *Portia* in which a specialized way of stalking salticids is known to have evolved.

In **Section IV**, there are three chapters (**Chapter 6 - 8**) in which I use *Portia labiata* and *Scytodes* sp. from Los Banos, in the Philippines, as a case

study and consider fine tuning of prey preference. In Los Banos, *P. labiata* routinely includes *Scytodes*, a spitting spider, in its diet. **Chapter 6** is concerned with the biology of *Scytodes*, including prey, predatory behaviour and maternal care. This provides background for studying capture behaviour and prey-preference of the Los Banos *P. labiata*. Of particular importance is that *Scytodes*, like *Portia*, is a predator on other spiders, and it preys especially on salticids. Spitting is a very effective predatory and anti-predatory behaviour, but brooding *Scytodes* carry their eggs in their fangs, effectively blocking their spitting weapons. In **Chapter 7**, I look at the interactions between *Scytodes* and four species of web-invading salticids, including Queensland *P. fimbriata*, Los Banos *P. labiata* and Sri Lanka *P. labiata*. This allows me to consider the efficiency of different salticids, with different predatory strategies, at catching *Scytodes*. That the Los Banos *P. labiata*, but not the other species of *Portia* and not other populations of *P. labiata*, appears to have evolved prey-specific capture behaviour for use against *Scytodes* is discussed. In **Chapter 8**, I consider fine tuning of preference behaviour (related to whether or not *Scytodes* is brooding) that has evolved in the Los Banos *P. labiata* and how these preferences reduce the danger to which this *Portia* is subjected by *Scytodes*.

In **Section V**, there is only one chapter (**Chapter 9**) in which I look at how preferred (*e.g.*, spiders) and less preferred prey (*e.g.*, insects) used as diets for rearing affect the specialized salticid's fitness expressed as survival rate in the Queensland *Portia fimbriata*. This is important information when considering the adaptive significance and ultimate causation of behavioural specialization in the context of optimal foraging theory.

Section VI (**Chapter 10** & **11**) is a discussion and synthesis. In **Chapter 10**, I clarify some of the features of a predator that may be 'specialized', and discuss the apparent match-up between prey-specific capture behaviour and prey preferences of the two groups of specialized salticids I studied: *i.e.*, the earlier chapters appear to show that, in myrmicophagic and in araneophagic species, when salticids have prey-specific capture behaviour for an unusual and dangerous prey, they seem also to prefer this prey. In **Chapter 11**, I consider evolutionary factors that may affect capture behaviour and prey preferences of

specialized predators, and discuss prey preferences in relation to optimal diet theory.

Some of the chapters in this thesis are co-authored paper in press. **Chapter 2** is a paper 'in press' in the *Journal of Zoology, London* co-authored with Drs Robert R. Jackson and Bruce Cutler. **Chapter 4** is a paper 'in press' in the *Journal of Insect Behavior*; **Chapter 10** is a paper prepared for the XIII International Congress of Arachnology (Geneva, Switzerland, September 1995) and it is 'in press' in the *Revue suisse de Zoologie*; both are co-authored with Dr Robert R. Jackson.

I am the senior authors of all of these co-authored papers. The senior author is, each time, the author who designed, carried out most of experimental tests and did the writing. The co-authors guided me on how to prepare the manuscripts in a style acceptable for publication. One of the authors (RRJ) made available to me some of the data used in two of these papers (**Chapter 2** & **4**). Dr Bruce Cutler (USA) supplied the ant-eating salticids (*Habrocestum pulex*) used for the study in **Chapter 2**, and his prior work on *H. pulex* provided advice that guided this study.

Some of the data in various chapters were made available to me by Dr Robert R. Jackson. I analyzed these data and included them with my own data sets. These data are field data on *Scytodes* in the Philippines (**Chapter 6**), data from testing salticids (using methods I designed and apparatus I built) in the Philippines and in Kenya using prey species from the field (**Chapter 5** & **6**) and tests of prey preferences of *H. pulex* using lacewings and mirids (**Chapter 2**). Over all, these were data which I could not obtain myself. For example, work with live Kenya and Philippines insects was not possible in New Zealand because of quarantine restrictions. However, having the opportunity to analyze these data and include them in the thesis was highly advantageous.

English is not my first language, and the style of writing appropriate for English-language scientific journals was not initially familiar to me. While writing this thesis, I received a lot of feedback on how to write. There were many drafts and many revisions. The repeated writing and re-writing were an important

learning exercise as part of my Ph.D. training.

SECTION II

MYRMICOPHAGIC SALTICIDS

CHAPTER 2

Prey-capture techniques and prey preferences of *Habrocestum pulex* (Hentz), an ant-eating jumping spider (Araneae: Salticidae) from North America

Abstract: The prey-capture techniques and prey preferences of *Habrocestum pulex*, an ant-eating jumping spider (Araneae: Salticidae) from North America, were studied in the laboratory. *H. pulex* uses prey-specific capture behaviour against ants. Ants, but not other insects, were consistently attacked head-on. After attacking an ant, but not after attacking other insects, *H. pulex* kept its forelegs extended laterally and forwards without touching the ground. *H. pulex* feeds on ants in preferences to other insects. Preference for ants and prey-specific capture behaviour do not depend on prior experience with ants. As in earlier studies of other ant-eating salticids, three different types of tests for prey preference were carried out, using active, living prey: type 1 (one type of prey presented to salticid at a time on alternate days); type 2 (two types of prey presented to salticid simultaneously and type 3 (salticid feeding on one type of prey presented with alternative prey of another type). However, newly-designed apparatus made testing more efficient. Preference for ants over other insects is shown not to depend on level of activity or any other cues from prey movement pattern: type 1 and type 2 tests were carried out using motionless (dead) lures, and again ants were taken in preference to other insects. Findings from this study are discussed in relation to recent findings on other ant-eating salticids.

Introduction

Recent studies of the myrmicophagic (Jackson & van Olphen, 1991, 1992) and araneophagic salticids (Jackson, 1992a; Jackson & Hallas, 1986a) suggest that, when predators evolve prey-specific capture behaviour for use against particularly dangerous and unusual prey that are not generally available to other related predators, they tend also to evolve a distinctive preference for these dangerous and unusual prey. In the present chapter I examine this hypothesis by studying *Habrocestum pulex* (Hentz).

Habrocestum pulex, a small (adult body length 3-4 mm), common salticid

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This chapter as manuscript submitted to the Journal of Zoology London 1995, has been acceptted and will come out this month. And referees wanted to provide more information about prey-specific capture behaviour of other ant-eating jumping spiders studied before. Also, as the first data chapter of the thesis, more detailed information, I think, can make sense for the readers. In fact, this kind of information suggests the hypothesis to test in this chapter and in the subsequent chapters.

in North America, frequents rock cutcrops and leaf litter in forest habitats where ants tend to be the most abundant salticid-size arthropods (see Hölldobler & Wilson, 1990). *H. pulex* has been reported to feed readily on worker ants in the field and in the laboratory (Fitch, 1963; Cutler, 1980). Tests in which *H. pulex* was given access simultaneously to ants, *Lasius crypticus* Wilson, and fruit flies, *Drosophila melanogaster* (Meigen) suggested, but failed to show conclusively, a preference for ants (Cutler, 1980). Also, the way in which *H. pulex* caught ants appeared to differ from the typical stalk-and-leap, prey-capture sequences of most salticids (Forster, 1977, 1982a), but detailed description of predatory sequences, based on video-tape analysis, has not been available. In the present study, I extend Cutler's (1980) earlier study by examining *H. pulex*'s prey-capture techniques in detail and by experimentally investigating this species' prey preferences.

H. pulex is an euophryine (Euophryinae) salticid. Other than *H. pulex*, the most thoroughly studied ant-eating salticids are another two euophryines, *Corythalia canosa* (Hentz) and *Zendorus* (formerly *Pystira*) *orbiculata* (Keyserling)(Edwards *et al.*, 1974; Jackson & van Olphen, 1991), and six heliophanines (Heliophaninae), *Chrysilla lauta* Thorell, *Siler semiglaucous* (Simon), *Natta rufopicta* (Simon) and another three species of *Natta* (Jackson & van Olphen, 1992). Prey-capture behaviour used against ants varies among the species. The six heliophanines are remarkably similar to each other, but differ from each of the two euophryines. Considering the euophryines, *Z. orbiculata* differs considerably in behaviour from *C. canosa*. *C. canosa* usually manoeuvres to attack ants head on. Heliophanines sometimes attack head on, but they also often attack from directly behind the ant. *Z. orbiculata* attacks ants from just about any orientation. However, *Z. orbiculata*, unlike the other ant-eating salticids, also often positions itself facing down on ant-infested tree trunks and ambushes ants by lunging down on them instead of actively pursuing them. *C. canosa* usually holds its cephalothorax elevated while pursuing, attacking and starting to feed on ants. The heliophanines, in contrast, tend to hold legs I, but not their cephalothoraces, elevated. When *C. canosa* and *Z. orbiculata* attack, they usually hold on, but the heliophanines often stab ants then back away.

These previously studied ant-eating salticids are behaviourally specialized on ants, but not restricted in diet to ants. They take other prey in typical salticid stalk-and-leap sequences (see Forster, 1982a). Also, there is consistent evidence from three different types of tests that each of the previously studied ant-eating salticids prefers ants to a variety of other prey (Jackson & van Olphen, 1991, 1992).

Salticids have complex eyes and acute vision (Land, 1969a, b; Blest *et al.*, 1990), suggesting that cues from prey shape alone might be sufficient for eliciting prey-specific capture behaviour and prey preferences. However, earlier studies (Jackson & van Olphen, 1991, 1992), in which only living, active prey were used, did not rule out cues from prey movement pattern and odour.

In the present study, I present data on *H. pulex* that are fully comparable to data available for the eight previously studied ant-eating salticids. However, we use new apparatus that facilitates testing of large numbers of spiders. Also, I extend the earlier work by testing *H. pulex* using equal-size motionless models (dried and coated dead prey), thereby ruling out cues from movement pattern and odour.

Materials and methods

For laboratory work I used cultures of *Habrocestum pulex* established from spiders collected from Kansas. Maintenance procedures, cage design, basic testing methodology and terminology were as in earlier studies (see Jackson & Hallas, 1986a; Jackson & van Olphen, 1991, 1992). Only essential details are given here. This includes the convention that the expressions 'usually' or 'often', 'sometimes', and 'occasionally' or 'rarely' are used to indicate frequencies of occurrence of >80%, 20-80% and <20%, respectively.

Insects used as prey were: fruit flies, *Drosophila melanogaster* (vestigial winged strain); lacewings, *Micromus tasmariae* (Walker)(Neuroptera, Hemerobiidae); mirid bugs, sp. indet (Hemiptera, Miridae); and workers of two species of ants - *Chelanes antarctica* and *Prolasius advera*. All insects were 2-3

mm in body length. The fruit flies were from laboratory cultures. The other insects were collected locally.

Tests of prey preference using living prey

Tests with living prey were carried out in a clear prey preference testing box (PPTB) made from plastic consisting of ten 80 X 80 X 20 mm (length X width X height) cells (Fig. 1). The top of the apparatus was transparent, but the sides of cells were opaque so that a *H. pulex* in one cell could not see into neighbouring cells. Each long side of the PPTB consisted of two pieces of plastic (an inner wall and an outer wall) 3 mm apart. Removable black cardboard screens fit between the inner wall and the outer wall. The apparatus had also two movable parts called 'comb'. Each comb consisted of ten 'teeth' (round wooden sticks 50 mm in length X 7 mm in diameter) extending from a plastic base. The ten teeth of the comb were positioned so that they could fit into the 10 plastic tubes (8 mm in diameter). Before testing began, one of the two tubes connected to each cell held a *H. pulex*; and the distal ends of every tube was stoppered by the tips of the teeth of the comb. The second tube on each cell was empty before and during Type 1 & 2 tests. However, in Type 3 tests, the second tube contained a prey item that was different from one in the cell (see below).

A prey item was put into each cell first and a spider was allowed to enter the cell about 10 min later to begin the test. The spider was first placed in one of the two tubes. To begin testing, the screen between the tubes and cells were removed and the two combs were pushed in slowly, forcing the ten *H. pulex* (and the 10 prey in Type 3 tests) into the cells. Once the spiders entered the cells, the screens were replaced.

Each test ended when the spider captured a prey or 15 min elapsed, whichever came first, except that observations continued until the sequence ended if the spider was in the act of pursuing a prey when the 15-min period elapsed. No individual spider was the subject in more than one test of any one type. Only adult females were tested. All spiders were fed only fruit flies prior to testing. 'Well-fed' and 'starved' spiders were kept without prey for 5 and 15 days, respectively, prior to testing. For each type of testing (see below), there was one

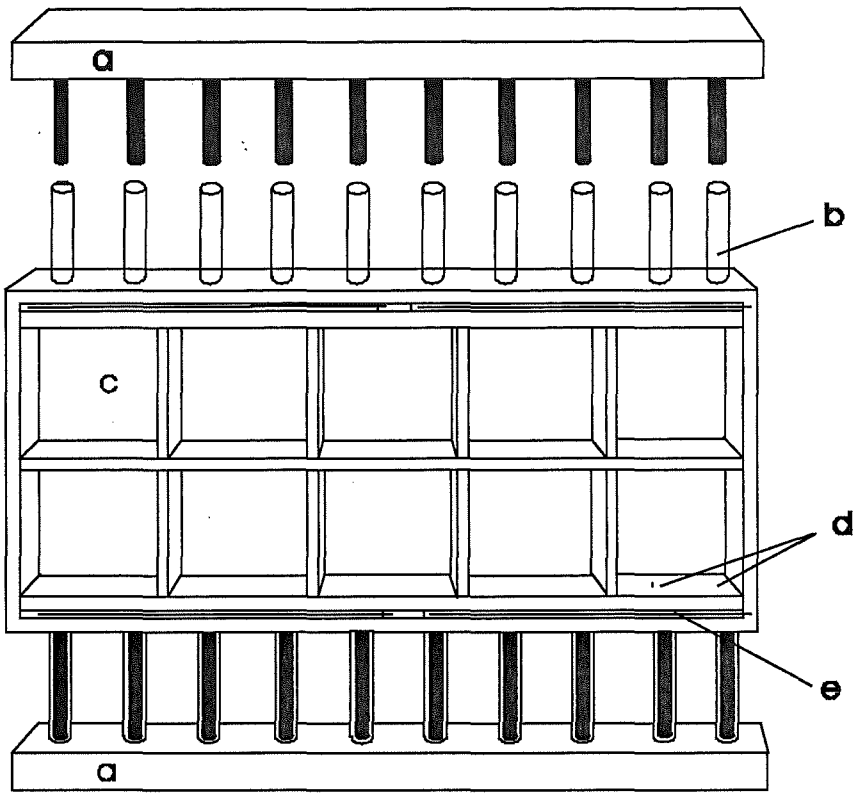

Fig. 1. Prey preference testing box (PPTB) used to test prey preferences of *Habrocestum pulex* using living, active prey. **a**: comb with 10 teeth (round wooden sticks; black in diagram) that could be moved horizontally for pushing *H. pulex* into cells (comb at top with teeth outside tubes; comb at bottom with teeth inside tubes); **b**: plastic tube; **c**: cell; **d**: 2 holes (diameter 8 mm) in the side of a cell; **e**: removable opaque cardboard screen. See text.

series of tests in which the spiders were well fed and one in which they were starved.

Testing on alternate days with one prey at a time (Type 1 tests)

Each spider was used in a pair of tests (one type of prey on one day and the other type on the following day). Half the spiders of each species were tested first with ants; the other half were tested first with fruit flies. Spiders were assigned randomly to the two groups.

Simultaneous testing with two prey (Type 2 tests)

One ant and one fruit fly were put into the cell at the same time and a spider was allowed to enter the cell to begin testing. The test ended when the spider took one of the two prey (*i.e.*, it was not allowed to take them both).

Feeding spider given an alternative prey (Type 3 tests)

In one test, a spider was given access to an ant while feeding on a fruit fly; in another test, the same spider was given access to fruit fly while feeding on an ant. Half the tested individuals was feeding on an ant first and half on a fruit fly first. Spiders were assigned randomly to the two groups.

The first prey was put in the cell and a spider was allowed to walk into the cell from the tube. If the spider began eating the prey with 15 min, a second prey was introduced 5 min later from another tube (containing the second prey) to the hole in the lateral side of the PPTB (Fig. 1). If the spider did not capture and begin feeding on the first prey within the allowed 15 min, the test was attempted again each day until it did so. This meant that a pair of tests was sometimes separated by more that 1 day (maximum interval that occurred: 4 days).

Tests of prey preference using motionless lures

The lure was a dead ant or a dead fruit fly, made by killing the ant or fruit fly by asphyxiation with CO_2, then placing it in alcohol for 1 hr. After mounting the lure on the centre of one side of a disc-shaped piece of cork (diameter *c.* 1.25 times the body length of the lure), the lure and the cork was sprayed with an

aerosol plastic adhesive for preservation and elimination of potential olfactory cues from the dead ant or fruit fly. If contacted by *Habrocestum pulex* during the test, the lure was washed with 80% ethanol and allowed at least 24 hr to dry before being used again.

In tests with motionless lures, a wooden choice ramp (CR) was used. The CR was a wooden apparatus consisting of a ramp and a base. Both the ramp and the base were Y-shaped and each had two arms (each arm 50 mm long and 40 mm wide) which angled at an angle of 40° and one tail (50 mm long and 50 mm wide) (Fig. 2). The wooden pole was 20 mm in diameter and was placed at 90 mm from the far end of the base tail so that the ramp angled up at an angle of 20°. The ramp was 15 mm thick and the base 12 mm thick.

The entire apparatus was painted with two coats of water-resistant polyurethane. Between each test, the ramp was wiped off with 80% ethanol, then allowed to dry for at least 30 min. This was to remove before the test possible chemical traces from previously tested *H. pulex*.

A piece of brown wood, 55 mm high and 40 mm wide, was glued to the top of each of the two arms on Y-shaped ramp. These pieces of wood served as a background against which *H. pulex* saw the lures. Also, a piece of hard cardboard, 55 mm high, was glued to outer side of each ramp arm (not shown in Fig. 2). This was to protect against *H. pulex* jumping off the apparatus. At the start of each test, one type of lure was presented at the centre of one arm of the Y-shaped ramp. At the centre of the other arm, there was either no lure (applicable to only Type 1 tests, see below) or the other type of lure. Each lure was 10 mm from the base of the backing wood.

A 200 W incandescent lamp, positioned *c.* 400 mm overhead, lit the entire apparatus; fluorescent ceiling lamps provided additional, ambient, lighting. The apparatus was surrounded by a white cardboard screen on three sides, the open side being for the observer. The ramp was positioned so that, during the test, *H. pulex* moved away from the open side and the observer.

There was a pit in the ramp (30 mm in diameter, centred 50 mm from the bottom end of the tail of Y-shaped ramp and 70 mm from the two lures). A piece of wood, covered with plastic, was glued to the bottom of the pit. Before the test,

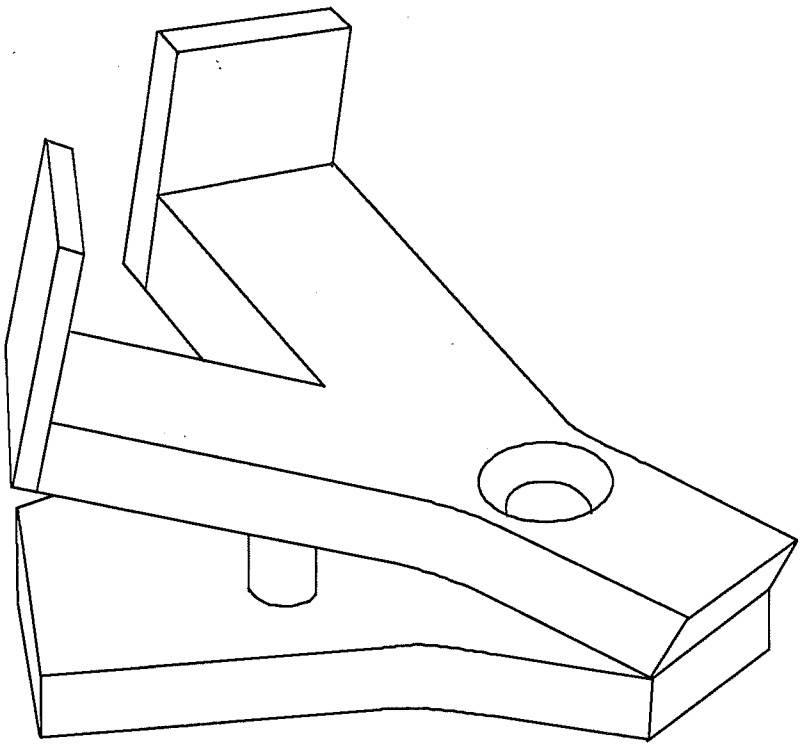

Fig. 2. The choice ramp (CR) used for testing prey preference of *H. pulex* using motionless lure. Test spider walks out of pit near bottom of ramp (circle on right of diagram) and up ramp towards motionless lures. See text.

H. pulex was placed in the pit. The lures were placed so that they were facing *c.* 45° away from the pit.

A *H. pulex* was placed in the pit and the pit was covered with a clear plastic petri dish until the *H. pulex* became quiescent. The pit was uncovered to start the test. The test was aborted if *H. pulex* stayed in the pit for 30 min or if, before reaching a line drawn below the joint of two Y-shaped ramp arms, the *H. pulex* moved off the ramp. When tests were aborted, the *H. pulex* was re-tested repeatedly, up to four times a day, then on subsequent days, until a successful test was completed or four days of unsuccessful testing elapsed. Each test ended when *H. pulex* did one of the following or 30 min elapsed, whichever came first, except that observation continued until the sequence ended if the spider was in the act of walking towards a lure when the 30-min period elapsed: 1) walked into the region of the ramp below the pit; 2) arrived at an arm on which no prey lure was present (applicable only to Type 1 tests, see below); 3) arrived at an arm on which a lure was present, but did not stalk lure, then moved off before reaching the lure; 4) arrived at an arm, then leapt on the backing wood without attacking the lure; 5) arrived at an arm, then stalked and approached the lure but failed to attack it; 6) arrived at an arm, then stalked and attacked the lure. Result 6 was rare. However, whenever result 4, 5, or 6 occurred, this was taken as evidence of prey choice.

Two of the testing methods used with live prey were duplicated when testing with motionless lures: Types 1 tests (testing on alternate days with one lure at a time) and Type 2 tests (simultaneously testing with two types of lures). In Type 1 tests, a lure was present on only one of the two arms of the Y-shaped ramp; the other arm was without a lure. The lure was placed on either the left or the right arm of the ramp (assigned randomly). In type 2 tests, an ant lure was placed at the centre of one arm of the ramp and a fly lure was placed at the centre of the other arm of the ramp.

Results

In the absence of prey, *H. pulex* normally walked in a rapid stop-and-go gait (*e.g.*, step for 0.5 s, pause for 0.5 s, etc.), rarely with palps and never with forelegs waving or abdomen bobbing. Palps were normally in a relaxed posture in front of the chelicerae, and al leg tarsi stayed on the ground except when stepping. When prey was present, if *H. pulex* attacked at all, it generally did so within 5 - 10 min. Predatory sequences against living fruit flies were usually different from sequences against living ants and will be described below.

Methods of catching living ants

Although *H. pulex* occasionally became activated when ants were either immobile or moving rapidly, *H. pulex* usually ignored ants that were immobile and avoided ants that are moving rapidly. *H. pulex* ignored and avoided ants for several seconds or minutes before becoming 'suddenly activated' (*i.e.*, a spider that had been ignoring, avoiding or perhaps orienting to watch an ant, suddenly began a prey-capture sequence without any obvious prelude). In a typical ant-catching sequence, *H. pulex* became suddenly activated and moved in spurts to get head on to the ant or up to 20° off from face to face, then lunged or made a short leapt from about a body length away. Typically, at the end of the lunge or leap, *H. pulex* stabbed the ant, released it immediately, then attacked again and so forth until eventually holding on to the ant. If a spider became suddenly activated at all, it generally did so within the first 5 min of a test, and once activated, these spiders usually attacked and fed on ants.

If *H. pulex* was activated and an ant was moving directly towards it, *H. pulex* tended to keep more or less stationary until the ant less than a body length away, then usually attacked by lunging. If *H. pulex* was activated and an ant moved past in front, *H. pulex* tended to keep up by running rapidly behind, then quickly circled the ant and attacked by lunging or leaping. If an ant was quiescent or moving especially slowly, *H. pulex*'s approach was often slower than normal locomotion.

Usually the spider made its attack on the ant when the spider and ant

were aligned face to face (occasionally), or the ant was about 20° off from face to face with the spider (usually).

While watching an ant from two or three body length away, *H. pulex* sometimes waved its palps slowly up and down in unison, but did not wave its forelegs. However, *H. pulex* always held its palps stationary, anterior and slightly lateral to the fangs, just before and during attack. During the attack, Legs I & II were usually arched forwards. Regardless of the ant's size, *H. pulex* tended to stab it after lunging or leaping, then, instead of holding on, retreated from the ant by walking backwards and attacked again several second later. These sequences were repeated (1 -2 times usually, occasionally up to 6 times) until the ant became more or less immobile or was moving only slowly; when this happened, the spider attacked head on. If a stabbed ant moved away rapidly, *H. pulex* usually did not pursue and attack it again.

At the end of an attack on an ant, *H. pulex*'s legs I & II were wrapped around the ant, but held off the ground. However, a few seconds later, *H. pulex* relaxed Legs II and placed them back on the ground as in normal posture, then several seconds after this, Legs I were relaxed and extended somewhat laterally and forwards, but kept held off the ground. Spiders usually bit the ant dorsally, most often on their petioles and thoraces, and only rarely on their heads and abdomens. When ant became quiescent (usually within 1 - 2 min after bitten), the spider fed on it first with mouthparts in the location on the ant's body at which the attack had been made. Later, the spider moved the ant around to feed from other locations on its body.

Methods of catching living fruit flies

In predatory sequences against fruit flies, sudden activation was not routine for *H. pulex*. The spiders usually began by orienting towards the fruit fly several times then attacking in sequences similar to the typical stalk-and-leap predatory sequences that have been described for other salticids (Forster, 1977, 1982a, b). While watching and approaching a fruit fly, the spider usually behaved more or less the same as in a normal locomotion. Spiders approached more or less directly and, when close, leapt. Leaps were usually from more than a body

length away. Attacks by lunging rather than leaping were rare. Legs and palps tended to remain in the normal posture both before and during attacks on fruit flies. *H. pulex* appeared to make no effort to orient attacks on fruit flies in any particular direction; attacks from the side, in front and behind were all about equally common. Legs I were kept on the ground in the normal posture after the attack. Although *H. pulex* occasionally stalked and attacked when fruit flies were either immobile or moving rapidly, *H. pulex* usually ignored fruit flies that were immobile and avoided fruit flies that were moving rapidly.

Stalking of motionless lures

Habrocestum pulex initially ignored the motionless lures, but eventually responded to them in much the same way as it responded to immobile living ants and fruit flies (*i.e.*, it performed its different prey-specific capture behaviours appropriately against each these two types of prey).

Tests for prey preference using living prey

When one prey type was presented at a time to the spider on alternate days (Type 1 tests), only those test-pairs in which the spider took one prey type but not the other provided evidence of prey preference. When two types of prey were presented simultaneously to the spider (Type 2 tests), a series of tests in which one type of prey was consistently taken more often than the other provided evidence of preference. When a feeding spider was given alternative prey (Type 3 tests), only those test-pairs in which the spider dropped one prey to take the other in one test but not the other of the two tests provided evidence of preference.

In tests on alternate days (Type 1 tests), when only one prey type was presented at a time, both well-fed and starved *H. pulex* attacked ants more often than other insects (TABLE I). Each spider ate every ant and other insects attacked.

In tests with simultaneously presented prey (Type 2 tests), well-fed and starved *H. pulex* attacked and ate ants more often than they attacked and ate other insects (TABLE II & III); 65 out of 70 spiders ate the ants they attacked,

and each spider that attacked a fruit fly or a mirid also ate it, but spiders never attacked lacewings.

In Type 3 test-pairs, both well-fed and starved *H. pulex* dropped other insects to take ants more often than they dropped ants to take other insects (TABLE IV).

TABLE I

Habrocestum pulex tested on alternate days (Type 1 tests) using living prey. Habrocestum pulex ate ants more often than they ate fruit flies

	Other insects	Ate ant only	Ate other insect only	Ate both	Ate neither	McNemar test[1]
Well-fed spider	Fruit fly	21	3	7	11	$P < 0.001$
	Lacewing	12	3	1	5	$P < 0.05$
	Mirid	7	0	5	4	$P < 0.01$
Starved spider	Fruit fly	18	1	8	2	$P < 0.001$

[1] Data in first two columns only used in these tests

TABLE II

Two prey presented simultaneously (Type 2 Tests) using living prey. Habrocestum pulex ate ants more often than they ate fruit flies

	Other insects	Ate ant	Ate other insect	Ate neither	Test of goodness of fit[1]
Well-fed spider	Fruit fly	23	8	8	$P < 0.01$
	Lacewing	6	0	5	$P < 0.05$
	Mirid	9	2	2	$P < 0.05$
Starved spider	Fruit fly	27	8	3	$P < 0.001$

[1] Data in first two columns only used in these tests

TABLE III

Two prey presented simultaneously (Type 2 Tests) using living prey Habrocestum pulex attacked ants more often than they attacked fruit flies

	Other insects	Attacked ant first	Attacked other insect first	Attacked neither	Test of Goodness of fit[1]
Well-fed spider	Fruit fly	24	8	8	$P < 0.005$
	Lacewing	7	0	4	$P < 0.01$
	Mirid	11	2	0	$P < 0.05$
Starved spider	Fruit fly	28	8	3	$P < 0.001$

[1] Data in first two columns only used in these tests

TABLE IV

Habrocestum pulex given second prey while feeding on first prey when using living prey

	Other insects	Drop other insect to eat ant	Drop ant to eat other insect	Drop each to eat other	Drops neither	McNemar test[1]
Well-fed spider	Fruit fly	13	2	1	34	$P < 0.01$
	Lacewing	7	1	0	9	$P < 0.05$
	Mirid	4	0	0	11	$P < 0.05$
Starved spider	Fruit fly	15	5	0	25	$P < 0.05$

[1] Data in first two columns only used in these tests

Tests for prey preference using motionless lures

In Type 1 tests (tests on alternate days) and Type 2 tests (tests in which prey were presented simultaneously), *H. pulex* chose lures made from dead, motionless ants more often than it chose lures made from dead, motionless fruit flies (TABLE V & VI).

TABLE V

Habrocestum pulex tested on alternate days (Type 1 tests) using motionless lures. H. pulex chose ant lures more often than it chose fly lures

	Chose ant only	Chose fly only	Chose both	Chose neither	McNemar test[1]
Well-fed spider	10	2	3	9	$P < 0.05$
Starved spider	12	3	5	4	$P < 0.05$

[1] Data in first two columns only used in these tests

TABLE VI

Two prey presented simultaneously (Type 2 tests) using motionless lures. Habrocestum pulex chose ant lures more often than it chose fly lures

	Chose ant	Chose fly	Chose neither	Test of goodness of fit[1]
Well-fed spider	12	4	5	$P < 0.05$
Starved spider	15	5	4	$P < 0.05$

[1] Data in first two columns only used in these tests

Discussion

It appears that *H. pulex* uses a different prey-specific capture behaviour depending on whether the prey is an ant or another insect. If the prey is an ant, 1) it is attacked more or less head-on and 2) forelegs are kept extended laterally and forwards after the attack. Other prey is attacked from the any directions and all of the spider's legs remain on the ground after the attack.

H. pulex has apparently evolved prey-specific capture behaviour for ants.

Some other salticids are known to have prey-specific capture behaviour for ants (Edwards *et al.*, 1974; Wing, 1983; Jackson & van Olphen, 1991, 1992). Based on the present and previous studies (Edwards *et al.*, 1974; Wing, 1983; Jackson & van Olphen, 1991, 1992), it seems that ant-eating salticids studied generally use different prey-specific capture behaviour depending on whether the prey is an ant or another type of insect. This is an example of predatory versatility (Curio, 1976), and predatory versatility is also known for some other salticids besides the ant-eating species (Jackson, 1992a; Edwards & Jackson, 1993), suggesting that predatory versatility may be widespread in this family of spiders.

Interestingly, *H. pulex* resembled another euophryine, *Corythalia canosa* (Jackson & van Olphen, 1991) by manoeuvring to attack the ant head on, then grabbing hold of the ant's thorax. However, unlike *C. canosa*, *H. pulex* never had its body raised while pursuing, attacking and starting to feed on ants. Also, *H. pulex*, unlike *C. canosa*, resembled previously studied heliophanines by frequently stabbing the ant one or more time before holding on. Also, *H. pulex*, in common with the other ant-eating salticids studied, appears to have a distinct preference for ants over other types of prey. Although prey-specific capture behaviour is different from prey preference and these could be independent each other, it appears that salticids that have evolved prey-specific capture behaviours for dangerous and unusual prey not normally available for other salticids have also evolved distinctive preferences for these prey. It was not obvious that this would be true on *a priori* grounds.

It is interesting that, in other ant-eating salticids studied, preference for ants was not as pronounced when the spider was starved, but there was no evidence of this in *H. pulex*. There is no obvious reason to account for *H. pulex* differing from the other species in this regard.

Ant-eating is unusual for a salticid. Most salticids probably tend to avoid ants (Cutler, 1980). This makes sense because ants are highly aggressive and often well-armed with poison, stings or strong mandibles. However, because ants are social insects which may be present in great abundance, a predator that once succeeds in overcoming the ant's defence will have access to a nearly unlimited food resource and few other spiders as competitors.

It appears appropriate to call *H. pulex* an 'ant specialist': ants are included in its diet in nature, it uses prey-specific capture behaviour to catch ants, and it prefers ants to other prey. However, it is important to remember that a predator's prey preferences is different from its prey-specific capture behaviour and also different from its diet in nature. Prey preference implies ability to distinguish between different potential prey types and choose to take one rather than the other. Preference is a behavioural trait of the animal and it cannot be inferred simply from knowing the animal's diet in nature (Jackson & van Olphen, 1991, 1992). In an earlier study (Cutler, 1980), there was suggestive, but inconclusive, evidence that *H. pulex* prefers ants. I were able to confirm in the present study that *H. pulex* clearly prefers ants to other prey by using the same three types of testing procedures applied earlier in studies of other ant-eating species (Jackson & van Olphen, 1991, 1992). In all of these studies, having showed consistent preferences with three different test designs justifies considerable confidence in the conclusions drawn. This combination of three testing procedures appears to be especially effective for testing prey preferences of ant-eating salticids.

Besides ant-eating salticids, a number of spider species from other families have also evolved prey-capture behaviours appropriate for overcoming the problems inherent in catching ants (Hingston, 1928; Mathew, 1954; Harkness, 1977; Oliveira & Sazima, 1984, 1985; Harkness & Harkness, 1992). Little is known currently about the preference of these non-salticid spiders, and it would be interesting to apply the methods developed for studies of ant-eating salticids to non-salticid spiders that eat ants. These studies would help to clarify whether the trend for prey-specific capture behaviour and prey preferences to evolve together, which appears to hold in the Salticidae, is also true of other spiders.

Potential cues by which most salticids distinguish between different types of prey include movement pattern, size and shape (Drees, 1952; Dill, 1975; Freed, 1984). However, some species are also known to initiate stalking and attacking and species with known prey preference and with prey-specific capture behaviours for different prey also known to discriminate between types of prey when prey is completely dead and motionless (Jackson & Tarsitano, 1993). *Corythalia canosa*, an ant-eating salticid, responded to ant lures and fly lures

made from dead, motionless prey in the same way that this species is known to respond to live ants and flies (*i.e.*,it showed its different prey-specific capture behaviours appropriately against these two types of prey) and also, attacked lures made from ants, this species' preferred prey, more often than other salticids attacked lures made from ants (Jackson & Tarsitano, 1993). In the present study, I provided evidence that *H. pulex* stalks and attacks motionless lures, using the same prey-specific capture behaviours observed in tests with live, motile prey, and shows the same prey preference (for ants) observed in tests with live, motile prey. Apparently, prey movement is not necessary for *H. pulex* to distinguish ants from other insects.

CHAPTER 3

Prey-capture techniques and prey preferences of five species of ant-eating jumping spiders (Araneae: Salticidae) from the Philippines

Abstract: Five species of salticids from the Philippines, *Chalcotropis* sp., *Euophrys* sp. 1 and 2, *Siler* sp., and *Telamonia masinloc*, routinely include in their diets ants, an unusual and dangerous prey for a salticid. The present paper is the first detailed study of the capture techniques and preferences of these five species. Each of these salticids used prey-specific capture behaviour against ants and different capture behaviour against a variety of other insects. Ants, but not other insects, were consistently attacked head-on by *Euophrys* sp. 1 and 2. *Siler* usually attacked from directly behind by stabbing several times before holding on. *Chalcotropis* and *Telamonia* attacked from just about any orientation. Three different types of tests for prey preference were carried out on each species. All five species fed on ants in preferences to other insects (*i.e.*, aphids, caterpillars, cockroaches, flies, moths, plant hoppers, psyllids and termites). These species' preferences for ants, and their prey-specific capture behaviour for catching ants, are shown not to depend on prior experience with ants. Results from this study are discussed in relation to recent findings on other specialized salticids.

Introduction

Jumping spiders (Salticidae) are commonly envisaged as generalist insectivores (*e. g.*, Foelix, 1982), but with an aversion to ants. However, there are two interesting minority groups of salticids, one that routinely feeds on ants (myrmicophagic species) (Edwards *et al.*, 1974; Cutler, 1980; Jackson & van Olphen, 1991, 1992) and another that routinely feeds on spiders (araneophagic species) (Jackson & Blest, 1982a; Jackson & Hallas, 1986a). Ants and spiders are interesting prey for salticids because ants and spiders have in common that they tend to be difficult-to-catch and dangerous for salticids (Robinson & Valerio, 1977; Jackson, 1992a).

Ants are prey-size arthropods (Hölldobler & Wilson, 1990) equipped with strong mandibles, poison-injecting stings or formic acid (Eisner, 1970; Blum, 1981), all of which seem to present formidable challenges to most cursorial spiders (Nentwig, 1986). Also, ants tend to be present in large numbers and can mount communal attacks on both prey and predators (Wilson, 1971). Nevertheless, there are a few salticids that routinely prey on ants (see Robinson & Valerio, 1977). The most thoroughly studied of these are three euophryines, *Corythalia canosa* (Hentz), *Habrocestum pulex* (Hentz)and *Zendorus* (formerly *Pystira*) *orbiculata* (Keyserling)(Edwards *et al.*, 1974; Cutler, 1980; Jackson & van Olphen, 1991), and six heliophanines, *Chrysilla lauta* Thorell, *Siler semiglaucous* (Simon), *Natta rufopicta* (Simon) and another three species of *Natta* (Jackson & van Olphen, 1992). Each of these nine ant-eating salticids studied, whether a euophryine or heliophanine, uses prey-specific capture behaviour against ants, behaviour which differs from how each captures other insects (Edwards *et al.*, 1974; Cutler, 1980; Jackson & van Olphen, 1991, 1992). Also, each has a pronounced preference for ants (Jackson & van Olphen, 1991, 1992). Whether this is a general trend in ant-eating salticids needs to be clarified by study of a wider range of species.

In the present study, I extend earlier work with a study of five species of ant-eating salticids from the Philippines. Knowledge of the Philippines spider fauna is rudimentary, and many new species and genera are likely to be discovered. Therefore, the names I use here should be viewed as tentative. In particular, the salticids called *Euophrys* sp. 1 and 2 almost certainly belong to an undescribed genus, and '*Euophrys*' is used merely as a convenient way of indicating that these spiders are euophryines. Each of these species has been seen eating ants in nature (Jackson, unpubl. data), but there have been no previous behaviour studies of any of these species and, except for *Siler*, any of these genera. Four of these species belong to previously studied subfamilies: *Chalcotropis* sp. and *Euophrys* sp. 1 and 2 are euophryines, and *Siler* sp. is a heliophanine. However, *Telamonia masinloc* Barrion & Litsinger is a plexippinine, and this is the first study of a plexippinine ant-eating salticid.

Salticids have complex eyes and acute vision (Land, 1969a, b; Blest *et al.*,

1990), suggesting that cues from prey shape alone might be sufficient for eliciting prey-specific prey-catching behaviour and prey preferences. However, except for a study on *Habrocestum pulex* (Chapter 2), only living, active prey have been used in earlier studies (Jackson & van Olphen, 1991, 1992). This has meant that, except for *H. pulex*, it has not been possible to rule out cues from prey movement pattern and odour as bases for preference. In the present study, all species studied are tested with both living insects and motionless lures.

For each species, using the testing methods applied successfully in the earlier studies (Jackson & van Olphen, 1991, 1992; Chapter 2), five questions are addressed:

1. How does it catch ants?
2. Does it use prey-specific capture behaviour depending on whether prey is an ant or another kind of insect?
3. Does it prefer ants to other insects?
4. Do its capture behaviour and prey preference depend on cues from different movement patterns of the different prey?
5. How does its predatory strategy compare to that of other ant-eating salticids?

Materials and methods

Siler sp. was found on rocks, leaf litter, tree trunks and the walls of buildings, usually near the ground. *Chalcotropis* sp. was found exclusively on trunks of large trees in rain forest. *Euophrys* sp. 1 and 2 and *Telamonia masinloc* were usually found on leaves and stems of trees and shrubs. Laboratory cultures were established from salticids collected in the field (some specimens of *Euophrys* sp. 2 were from Subic Bay; other specimens of *Euophrys* sp. 2 and all specimens of all other species were from Los Banos) in Luzon, the Philippines (TABLE I). Data presented here came from studies on laboratory cultures in Los Banos (International Rice Research Institute) and in Christchurch, New Zealand (Zoology Department, University of Canterbury) using a variety of ants and other

insects as prey in prey-preference tests (TABLE II).

Maintenance procedures, cage design, basic testing methods and terminology were as in earlier salticid studies (see Jackson & Hallas, 1986a; Jackson & van Olphen, 1991). This included the convention that expressions 'usually', 'sometimes', and 'rarely' were used to indicate frequencies of occurrence of >80%, 20-80% and <20%, respectively. Spiders were reared on a variety of insect prey, but had no experience with ants prior to laboratory testing.

TABLE I

Ant-eating salticids studied in the laboratory

Species	Subfamily	Collection site	Adult body length (mm)
Euophrys sp. 1	Euophryinae	Subic Bay, Los Banos	2-3
Euophrys sp. 2	Euophryinae	Los Banos	2-3
Siler sp.	Heliophaninae	Los Banos	4-5
Chalcotropis sp.	Euophryinae	Los Banos	4-6
Telamonia masinloc	Plexippininae	Los Banos	5-7

Tests of prey preference using living prey

Tests in Christchurch were carried out using the prey preference testing box (PPTB) described elsewhere (Chapter 2), whereas tests in Los Banos were carried out using petri dishes, as described by Jackson & van Olphen (1991). All spiders were fed only fruit flies prior to testing. In all tests, the goal was to determine whether the salticid took ants in preference to another type of insect. For each type of testing (see below) and for each species of spider, when the other insect was an aphid or a fruit fly, there was one series of tests in which the spiders were well fed and one in which they were starved. 'Well-fed' and 'starved' spiders were kept without prey for 5 and 15 days, respectively, prior to testing.

A test began when the spider entered the petri dish or a cell in the box (PPTB) and ended when the spider captured a prey or 15 min elapsed,

TABLE II

Insects used in the laboratory as living prey and motionless lures

Description	Order	Family	Species	Body size	Origin	Use
Ant workers	Hymenoptera	Formicidae	*Anoplolepsis* sp	7 mm	Philippines	Live prey & lure
			Campanotus sp	3-7 mm	Philippines	Live Prey & lure
			Chelaner antarctica	3-4 mm	New Zealand	Live prey
			Diacammon sp	12 mm	Philippines	Live prey & lure
			Iridomyrmex darwianus (Forel)	2 mm	New Zealand	Live prey
			Oecophylla smaragdina (Fabricius)	7-8 mm	Philippines	Live prey & lure
			Pheidologeton sp	4-5 mm	Philippines	Live prey & lure
			Polyrachis sp	5-6 mm	Philippines	Live prey & lure
			Solenopsis geminata	4 mm	Philippines	Live prey & lure
			Tapinoma melanocephala (Fabricius)	1-2 mm	Philippines	Live prey
Aphid nymphs & adults	Hemiptera (suborder Homoptera)	Aphidae	*Macrosiphum euphorbiae* (Thomas)	1-3 mm	New Zealand	Live prey
Brown Plant hopper nymphs & adult	Hemiptera (suborder Homoptera)	Dephacidae	*Niloparvata lugens* (Stal)	2-3 mm	Philippines	Live prey & lure
Green leaf hopper nymphs & adults	Hemiptera (suborder Homoptera)	Cicadellidae	*Nephotettix nigropictus* (Stal)	2-5 mm	Philippines	Live prey & lure
Psyllid nymphs & adults	Hemiptera (suborder Homoptera)	Psyllidae	*Heteropsylla cubana* Crawford	1-2 mm	Philippines	Live prey
Leaffolder caterpillars	Lepidoptera	Pyralidae	*Cnaphalocrocis medinalis* Guenee	2-6 mm	Philippines	Live prey
Stemborer caterpillars	Lepidotpera	Pyralidae	*Chilo suppressalis*	3-6 mm	Philippines	Live prey

TABLE II continues

Description	Order	Family	Species	Body size	Origin	Use
Cockroach nymphs		Blatteridae	Unknown	4-7 mm	Philippines	Live prey
Fly	Diptera	Drosophilidae	*Drosophila melanogaster* (Meigen)	2-3 mm	Laboratory culture	Live prey
		Muscidae	*Musca domestica* (Linnaeus)	6-8 mm	Laboratory culture	Live prey & lure
		Ephydridae	*Notiphila* sp	3 mm	Philippines	Live prey & lure
		Dolichopodidae	Unknown	2-4 mm	Philippines	Live prey & lure
		Stratiomyidae	Unknown	4-6 mm	Philippines	Live prey & lure
Lacewing	Neuroptera	Chrysopidae	*Chrysopa* sp	3-5 mm	Philippines	Live prey
Moth	Lepidoptera	Pyralidae	*Chilo suppressalis*	13-16 mm	Philippines	Live prey & lure
		Pyralidae	*Cnaphalocrocis medinalis* (Guenee)	10-12 mm	Philippines	Live prey & lure
		Pyralidae	*Diaphania indica* (Saunders)	11-14 mm	Philippines	Lure
		Pyralidae	*Marasima patnalis* Bradley	9-11 mm	Philippines	Lure
		Noctuidae	*Naranga aerescens* Moore	9 mm	Philippines	Lure
Termite worker	Isoptera	Termitidae	Unknown	3-5 mm	Philippines	Live prey

whichever came first, except that observations continued until the sequence ended if the spider was in the act of pursuing a prey when the 15-min period elapsed. No individual spider was the subject in more than one test of any one type. Only adults females were tested.

In all tests, the ant and the other insect were always of matching size. The variety of insect species used made this possible. In all tests, the insects were between half and equal to the size of the spiders in estimated body volume.

Type 1 tests (testing on alternate days with one prey at a time)

Each spider was used in a pair of tests (one type of prey on one day and the other type on the following day). Half the spiders of each species were tested first with ants; the other half were tested first with other insects. Spiders were assigned to the two groups randomly.

Type 2 tests (testing simultaneously with two prey)

One ant and one other insect were put into a petri dish or box cell at the same time, then a spider was allowed to enter to begin testing. The test ended when the spider took one of the two prey (*i.e.*, the spider was not allowed to take them both).

Type 3 tests (testing feeding spider with an alternative prey)

In one test, a spider had access to an ant while feeding on an other insect on one day; in another test, on alternative day, the same spider had access to other insect while feeding on an ant. Half the tested spiders of each species were feeding on an ant first and half on the other insect first. Spiders were assigned randomly to the two groups.

Tests of prey preference using motionless lures

Methods were identical to tests using lures carried out previously on *Habrocestum pulex* except that only Type 1 tests (testing on alternate days with one lure at a time), instead of Type 1 and 2 tests, were carried out and the choice ramp (CR) was simpler. In Chapter 2, the CR consisted of two arms on

a Y-shaped ramp. In the present Chapter, the CR was a single platform ('arm') 100 mm long and 40 mm wide angled up at 20°. As in the earlier study, a piece of brown wood glued to the top of the ramp served as a background against which the salticids saw a lure centred on the ramp 10 mm from the base of the wood. As in the Chapter 2, lures were made from dead insects (TABLE II) made by killing the insect by asphyxiation with CO_2, placing it in alcohol for 1 hr, then mounting it on the centre of one side of a disc-shaped piece of cork (diameter *c.* 1.25 times the body length of the lure) and spraying the lure and the cork with an aerosol plastic adhesive for preservation and elimination of potential olfactory cues from the dead insect. However, a greater variety of insects was used to make the lures in the present than in the earlier study (TABLE II).

Analysis of prey preference data

When, on alternate days, one prey type at a time was presented to the spider (Type 1 tests), only those test-pairs in which the spider took one prey type but not the other provided evidence of prey preference. When two types of prey were presented simultaneously to the spider (Type 2 tests), a series of tests in which one type of prey was consistently taken provided evidence of preference. When a feeding spider was given alternative prey (Type 3 tests), only those test-pairs in which the spider dropped one prey to take the other, but not vice versa, provided evidence of prey preference.

As there was no evidence that data from the two populations of *Euophrys* sp. 1 differed, these data sets were pooled and the pooled data are referred to simply as '*Euophrys* sp. 1'.

Results

In the absence of prey, *Siler* sp. normally walked, as described earlier (Jackson & van Olphen, 1992) for *Siler semiglaucous*, in a rapid stop-and-go gait (*e.g.*, step for 0.5 s, pause for 0.5 s, etc.), with palps and legs I waving and abdomen bobbing up and down both while stepping and while pausing (see

Jackson & van Olphen, 1992). Palps were usually waved rapidly (*c.* 5/s) and more or less continuously, whereas legs I were waved more slowly (*c.* 1/s) and only intermittently. During pauses, *Siler* sometimes stood with legs I elevated and waving, abdomen flexed up but not bobbing, or both. *Chalcotropis* sp., *Euophrys* sp. 1 and 2, and *Telamonia masinloc* walked in a rapid stop-and-go gait, without waving their palps and legs and without bobbing their abdomen while stepping or while pausing.

Each of these five species responded to ants differently from how it responded to other insects. Although these sequences were not observed in detail, it was clear that responses of these five salticids to all of the different species of ants used (TABLE II) were basically same. However, there was distinct variation among the five salticids in capture behaviour used against ants. Also, for each of these five salticids, the way ants were attacked differed from other insects were attacked.

Methods used by Euophrys sp. 1 and 2 to catch ants

Initially, *Euophrys* sp. 1 and 2 tended to ignore quiescent ants and avoid active ants, or they might watch an ant, all the while keeping distant from it. However, after several seconds or minutes, the salticid might become 'suddenly activated' (see Jackson & van Olphen, 1991, 1992): begin a prey-capture sequence without obvious prelude. If a *Euophrys* sp. 1 or 2 became suddenly activated at all, it generally did so within the first 5 min of a test, and once activated, these spiders usually attacked and fed on ants.

From the start, the *Euophrys* sp. 1 or 2 repeatedly manoeuvred around, backed off and followed the active ant to achieve head-on orientation. Movement was usually in a series of bursts of *c.* 5 mm each. Stepping tended to be to the side more or less on an arc. Once head-on, the spider lunged or made a short leap onto the ant, without pausing first, from about half a body length away, and held on to the ant's dorsal thorax.

When attacking ants, the salticid's legs I and II, and its palps, were usually held down and wrapped around the ant. However, a few second later, the spider usually relaxed legs II and placed them back on the ground as in the normal

walking posture, then several seconds after this, legs I were relaxed further and extended somewhat laterally and forwards.

Methods used by Euophrys 1 and 2 to catch other insects

Euophrys sp. 1 and 2 usually began by orienting towards the other insect several times, then attacked in sequences different from the sequences against ants, but similar to the typical stalk-and-leap predatory sequences that appear to be prevalent in non-specialized salticids (Forster, 1977, 1982a). While watching and approaching the insect, *Euophrys* sp. 1 or 2 usually kept legs on the ground and palps stationary in front of the chelicerae, and approached more or less directly. When close (about one and half body length away from the insect), the spider leapt, with or without pausing first.

Euophrys sp. 1 and 2 appeared to make no effort to achieve any particular orientation with the insects before attacking: the spider attacked from the side, in front or behind the insect about equally often. During the attack, the salticid's forelegs were extended laterally. However, at the end of the attack, salticid's forelegs were usually in the normal rest posture or, if the prey struggled vigorously, wrapped around the prey.

Methods used by Siler sp. to catch ants

As for *Euophrys* sp. 1 and 2, for *Siler* sp., after a period of avoiding, ignoring or simply watching the ant, there was a sudden change from being passive to active pursuit ('sudden activation'), and if *Siler* sp. attacked at all, it generally did so within the first 5 - 10 min of the test. Once activated, *Siler* sp. almost always caught the ant.

From the start, *Siler* sp. tended to approach the ant from the rear, repeatedly manoeuvring around, backing off and following the ant to achieve a from-behind approach. Spiders kept up with fast-moving ants by themselves moving rapidly and agilely. If an ant was quiescent or moving only slowly, the approach of *Siler* sp. was often slower than normal locomotion. When an ant approached to within a distance of 10-20 mm, *Siler* sp. usually backed away and simultaneously veered to the side, then manoeuvred to get behind and again

followed the ant. While directly behind the ant, *Siler* sp. lunged (usually) or made a short leap (rarely) from behind and stabbed (fangs briefly penetrate prey's body), then released, the ant. Head-on attacks by *Siler* sp. were initially rare. However, once successive stabbing attacks noticeably weakened the ant, head-on attacks were more common.

Sometimes, while *Siler* sp. was oriented toward the rear of an ant, the ant turned around, faced the spider and moved toward it. When this happened, the spider moved to get behind the ant again. When this was difficult (*e.g.*, if an ant was close to a wall of the testing arena), the spider rarely attacked.

After a stabbing attack from behind, the spider immediately released the ant and backed away 10-20 mm. If the ant continued walking, the spider usually followed 10-50 mm behind. If the ant ran away, the spider might initially just watch the ant before rapidly closing the distance to come up again from behind. If the ant remained very active despite repeated stabs, the spider eventually lunged or leapt and held on to the ant. However, if the ant became noticeably less active, though not completely quiescent, after being stabbed, *Siler* sp. stopped attacking. Instead, *Siler* sp. watched the ant from 20-40 mm away for 2-4 min until it became nearly or completely immobile.

Once the ant was more or less immobilized, *Siler* sp. usually approached it slowly, and manoeuvred to get in front. *Siler* sp. usually attained a front position by circling until properly aligned. Next, *Siler* sp. almost always lunged from a distance of about a half body length away and, with its chelicerae and fangs, grabbed the ant's antennae, then pulled the ant away by walking backward 5-15 mm. By pulling on the ant's antenna, *Siler* sp. kept away from ant's mandibles and made it difficult for the ant to defend itself. Immediately after taking hold of the ant, *Siler* sp. usually kept its legs I off ground, but after the attacked ant's struggles subsided, *Siler* stopped pulling the ant and used legs I and II to hold the ant down.

Siler sp. waved its legs and palps, and bobbed its abdomen during normal locomotion and while stalking ants. Also, during and immediately after the attack on an ant, *Siler* sp. usually kept legs elevated. While feeding, *Siler* sp. usually rested its palps on the ant, but kept legs I raised and waving.

Methods used by Siler sp. to catch other insects

As was the case for *Euophrys* sp. 1 and 2, in predatory sequences against other insects, 'sudden activation' was not routine for *Siler* sp. Instead, *Siler* sp. usually attacked other insects in sequences more or less similar to how typical salticids attack prey (Forster, 1982a) except that leg waving was more pronounced than typical for salticids in general. While watching or approaching an insect, *Siler* sp. usually waved its palps and legs and bobbed its abdomen, as in normal locomotion, and approached more or less directly. When about one or two body length away, *Siler* sp. paused then leapt on the insect from in front, the side or behind. Attacks by lunging rather than leaping were rare. When attacking, legs I were only rarely elevated, but *Siler* often waved these legs or held them elevated afterwards.

Methods used by Chalcotropis sp. to catch prey

Chalcotropis sp. had two modes of prey-capture: active pursuit and ambush. In active pursuit, *Chalcotropis* sp. fixated its anterior median eyes on its prey, approached it rapidly, then leapt on it, with or without first pausing. Leaps tended to be from 1-5 body lengths away. *Chalcotropis* sp. tended neither to raise nor lower its body during these pursuits, and it kept its legs and palps in more or less the normal posture. *Chalcotropis* sp. used its chelicerae to seize the prey but rarely spread legs out to the side.

Predation by *Chalcotropis* sp. in the laboratory was usually by active pursuit. Active pursuit of prey was also seen in the field, but more often *Chalcotropis* sp. was seen ambushing prey in the field. In the field, *Chalcotropis* sp. stood on tree trunks, facing downward, and ambushed ants that walked by below them. Ants were very numerous on these tree trunks. To ambush an ant, *Chalcotropis* sp. lunged downward, or made a short leap downward (usually no more than two body lengths), onto the ant. The spider kept a dragline fastened to the tree during the attack and, at the end of the lunge or leap, the spider stepped backward to return to the position from which it began.

In both the field and the laboratory, *Chalcotropis* sp. readily caught ants and other insects by active pursuit, but only ants were attacked by ambush. Upon

seeing ants, *Chalcotropis* sp. would move close, position itself facing down, then remain stationary. It did not respond in this way to other insects.

Methods used by Telamonia masinloc to catch prey

The salticid usually fixated its AM eyes on the prey, approached it rapidly, then leapt on it from 1-8 body lengths away, with or without first pausing. When approaching and attacking, the spider tended to keep its legs and palps stationary in more or less the normal posture. In these active pursuits, the spider's attack was oriented more or less front-on when the prey was an ant but, when the prey was some other insects, it tended to be indiscriminately from the side, behind or the front.

Stalking of motionless lures

Each salticid species initially ignored the motionless lures, but eventually responded to them in much the same way as it responded to living ants and other insects (*i.e.*, it performed its different prey-specific capture behaviours appropriately against each type of lure).

Tests for prey preference using living prey

In tests on alternate days (Type 1 tests) using living prey, when only one prey type was presented at a time, well-fed and starved salticids of all species studied ate ants more often than other insects (TABLE III), except that starved *Telamonia masinloc* ate ants and aphids and, ants and flies, at comparable rate ($P < 0.1$ and $P < 0.1$, respectively). Each time, the salticid ate the prey it initially attacked.

In tests with simultaneously presented prey (Type 2 tests), well-fed and starved salticids of each species attacked living ants first more often than they attacked other living insects first (TABLE IV). Each time, the salticid ate the ant and other insect it initially attacked.

In Type 3 test-pairs using living prey, well-fed salticids of each species dropped other insects to take ants more often than they dropped ants to take other insects. Except for starved *Euophrys* sp. 1 and 2, *Chalcotropis* sp. and

Telamonia masinloc tested with fruit flies (*Drosophilia melanogaster*) and aphids, starved *Siler* sp. dropped fruit flies (*D. melanogaster*) and aphids to take ants more often than it dropped ants to take fruit flies and aphids, and starved salticids of each species dropped moths (adults) and plant hoppers to take ants more often than they dropped ants to take moths and plant hoppers (TABLE V).

Tests for prey preference using motionless lures

In tests on alternate days (Type 1 tests), each salticid species chose lures made from dead, motionless ants more often than it chose lures made form other kinds of insects (TABLE III).

TABLE III

Results from Type 1 tests (salticids tested on alternate days) showing that ants were eaten more often than other insects. Except for tests in which lures were used, all data are from using living prey

Salticid	Hunger state	Ant	Other insect	Ate ant only	Ate other insect only	Ate both	Ate neither	McNemar test
Euophrys sp. 1	Well fed	*I. darwinanus*	Aphid	19	1	6	0	$P < 0.001$
		T. melanocephala	Brown plant hopper	12	2	9	1	$P < 0.01$
		T. melanocephala	Brown Plant hopper lure	10	2	2	5	$P < 0.05$
		T. melanocephala	Psyllid	14	4	7	2	$P < 0.05$
		Campanotus	Caterpillar (*C. medinalis*)	10	0	2	6	$P < 0.005$
		I. darwinanus	Fly (*D. melanogaster*)	19	1	7	2	$P < 0.001$
		Campanotus	Termite	21	7	1	8	$P < 0.01$
	Starved	*I. darwinanus*	Aphid	21	2	17	0	$P < 0.001$
		T. melanocephala	Psyllid	13	4	15	0	$P < 0.05$
		I. darwinanus	Fly (*D. melanogaster*)	21	2	18	0	$P < 0.001$
Euophrys sp. 2	Well fed	*I. darwinanus*	Aphid	10	0	3	0	$P < 0.005$
		T. melanocephala	Brown plant hopper	14	4	7	2	$P < 0.05$
		T. melanocephala	Brown Plant hopper lure	10	2	0	4	$P < 0.05$
		T. melanocephala	Psyllid	10	1	9	0	$P < 0.01$
		Campanotus	Caterpillar (*C. medinalis*)	8	0	5	3	$P < 0.01$
		I. darwinanus	Fly (*D. melanogaster*)	10	0	3	0	$P < 0.005$
		Campanotus	Termite	10	1	6	0	$P < 0.01$

TABLE III continues

Salticids	Hunger state	Ant	Other insect	Ate ant only	Ate other insect only	Ate both	Ate neither	McNemar test
Euophrys sp. 2	Starved	*I. darwinanus*	Aphid	15	0	11	0	$P < 0.001$
		T. melanocephala	Psyllid	12	3	17	0	$P < 0.05$
		I. darwinanus	Fly (*D. melanogaster*)	15	0	11	0	$P < 0.001$
Chalcotropis sp.	Well fed	*C. antarctica*	Aphid	11	0	4	0	$P < 0.001$
		Campanotus	Brown plant hopper	8	0	4	2	$P < 0.01$
		Campanotus	Brown plant hopper lure	10	0	0	3	$P < 0.005$
		S. geminata	Caterpillar (*C. medinalis*)	11	1	1	2	$P < 0.01$
		Pheidologeton	Caterpillar (*C. suppressalis*)	13	2	4	6	$P < 0.01$
		Campanotus	Cockroach	8	0	1	4	$P < 0.01$
		C. antarctica	Fly (*D. melanogaster*)	10	0	4	0	$P < 0.005$
		Polyrachis	Fly (*M. domestica*)	7	0	5	5	$P < 0.01$
		Campanotus	Fly (Dolichopodid)	12	3	2	2	$P < 0.05$
		S. geminata	Fly (Stratiomyid)	10	1	3	2	$P < 0.01$
		Campanotus	Lacewing	7	0	6	3	$P < 0.01$
		O. smaragdina	Moth (*C. medinalis*)	19	5	0	5	$P < 0.01$
		Campanotus	Fly (Notiphila)	9	0	2	10	$P < 0.005$
		Campanotus	Termite	15	5	8	3	$P < 0.05$
	Starved	*I. darwinanus*	Aphid	9	0	5	0	$P < 0.005$
		Campanotus	Brown plant hopper	10	2	0	22	$P < 0.05$
		Campanotus	Fly (*D. melanogaster*)	6	0	10	0	$P < 0.05$

TABLE III continues

Salticid	Hunger state	Ant	Other insect	Ate ant only	Ate other insect only	Ate both	Ate neither	McNemar test
Siler sp.	Well fed	*I. darwinanus*	Aphid	5	0	0	9	$P < 0.05$
		Campanotus	Brown plant hopper	10	0	0	16	$P < 0.005$
		Campanotus	Brown plant hopper lure	15	5	10	1	$P < 0.05$
		T. melanocephala	Psyllid	6	0	1	5	$P < 0.05$
		S. geminata	Caterpillar (*C. medinalis*)	7	0	0	12	$P < 0.01$
		C. antarctica	Fly (*D. melanocephala*)	8	1	0	6	$P < 0.05$
		Campanotus	Fly (Notiphila)	9	2	1	7	$P < 0.05$
		Campanotus	Fly lure (Notiphila)	6	0	2	3	$P < 0.05$
		Campanotus	Fly (Dolichopodid)	7	0	2	2	$P < 0.01$
		Campanotus	Fly lure (Dolichopodid)	5	0	1	6	$P < 0.05$
		Campanotus	Termite	19	6	10	9	$P < 0.01$
	Starved	*I. darwinanus*	Aphid	5	0	0	8	$P < 0.05$
		C. antarctica	Fly (*D. melanogaster*)	7	1	0	5	$P < 0.05$
		Campanotus	Brown plant hopper	10	0	0	16	$P < 0.005$
Telamonia masinloc	Well fed	*C. antarctica*	Aphid	7	1	2	0	$P < 0.05$
		Campanotus	Brown plant hopper	18	7	6	2	$P < 0.05$
		Campanotus	Brown plant hopper lure	11	2	1	4	$P < 0.05$
		Pheidologeton	Green leaf hopper	13	4	8	2	$P < 0.05$
		Pheidologeton	Green leaf hopper lure	5	0	3	10	$P < 0.05$
		Campanotus	Caterpillar (*C. medinalis*)	7	0	0	12	$P < 0.01$

TABLE III continues

Salticid	Hunger state	Ant	Other insect	Ate ant only	Ate other insect only	Ate both	Ate neither	McNemar test
Telamonia masinloc	Well fed	*Campanotus*	Caterpillar (*C. suppressalis*)	10	2	2	7	$P < 0.05$
		Campanotus	Cockroach	14	4	6	1	$P < 0.05$
		C. antarctica	Fly (*D. melanogaster*)	8	1	6	2	$P < 0.05$
		O. smaragdina	Fly (*M. domestica*)	15	5	2	0	$P < 0.05$
		O. smaragdina	Fly lure (*M. domestica*)	9	1	2	8	$P < 0.05$
		Campanotus	Fly (Notiphila)	7	1	5	0	$P < 0.05$
		Campanotus	Fly lure (Notiphila)	9	0	2	10	$P < 0.005$
		Campanotus	Fly (Dolichopodid)	11	2	10	2	$P < 0.05$
		Campanotus	Fly lure (Dolichopodid)	8	0	1	13	$P < 0.01$
		Polyrachis	Fly (Stratiomyid)	6	0	2	5	$P < 0.05$
		Polyrachis	Fly lure (Stratiomyid)	5	0	4	9	$P < 0.05$
		Campanotus	Lacewing	10	2	5	0	$P < 0.05$
		Diacammon	Moth (*C. suppressalis*)	8	0	0	18	$P < 0.01$
		Diacammon	Moth lure (*C. suppressalis*)	5	0	5	5	$P < 0.05$
		Diacammon	Moth lure (*D. indica*)	5	0	2	10	$P < 0.05$
		O. smaragdina	Moth lure (*M. patnalis*)	9	1	0	12	$P < 0.05$
		O. smaragdina	Moth lure (*N. aerescens*)	5	0	0	16	$P < 0.05$
		Diacammon	Moth lure (*N. aerescens*)	6	0	1	13	$P < 0.05$
		Campanotus	Termite	8	1	13	0	$P < 0.05$
	Starved	*C. antarctica*	Aphid	6	2	3	0	NS

TABLE III continues

Salticid	Hunger state	Ant	Other insect	Ate ant only	Ate other insect only	Ate both	Ate neither	McNemar test
Telamonia masinloc	Starved	*C. antarctica*	Fly (*D. melanogaster*)	9	4	4	0	NS
		Campanotus	Moth (*C. suppressalis*)	6	0	4	2	$P < 0.05$
		Campanotus	Brown plant hopper	7	0	0	12	$P < 0.01$

TABLE IV

Results from Type 2 tests (salticids tested with two prey simultaneously) showing that ants were eaten more often than other insects. All data from using living prey

Salticid	Hunger state	Ant	Other insect	Ate ant	Ate other insect	Ate neither	Test of Goodness of fit
Euophrys sp. 1	Well fed	*I. darwinanus*	Aphid	40	5	2	$P < 0.001$
		T. melanocephala	Brown plant hopper	13	2	2	$P < 0.01$
		Campanotus	Caterpillar (*C. medinalis*)	10	1	7	$P < 0.01$
		I. darwinanus	Fly (*D. melanogaster*)	27	4	0	$P < 0.001$
		T. melanocephala	Psyllid	15	3	2	$P < 0.01$
	Starved	*I. darwinanus*	Aphid	34	4	2	$P < 0.001$
		I. darwinanus	Fly (*D. melanogaster*)	27	4	0	$P < 0.001$
Euophrys sp. 2	Well fed	*I. darwinanus*	Aphid	29	2	1	$P < 0.001$
		T. melanocephala	Brown plant hopper	12	2	0	$P < 0.01$
		Campanotus	Caterpillar (*C. medinalis*)	10	0	5	$P < 0.005$
		I. darwinanus	Fly (*D. melanogaster*)	13	3	6	$P < 0.05$
		T. melanocephala	Psyllid	7	1	4	$P < 0.05$
	Starved	*I. darwinanus*	Aphid	21	2	2	$P < 0.001$
		I. darwinanus	Fly (*D. melanogaster*)	11	2	4	$P < 0.05$
Chalcotropis sp.	Well fed	*C. antarctica*	Aphid	15	3	2	$P < 0.01$
		Campanotus	Brown plant hopper	12	3	2	$P < 0.05$
		S. geminata	Caterpillar	8	0	9	$P < 0.01$

TABLE IV continues

Salticid	Hunger state	Ant	Other insect	Ate ant	Ate other insect	Ate neither	Test of Goodness of fit
Chalcotropis sp.	Well fed	*C. antarctica*	Fly (*D. melanogaster*)	16	4	0	$P < 0.01$
		Polyrachis	Fly (*M. domestica*)	6	0	5	$P < 0.05$
		Campanotus	Fly (Notiphila)	9	1	6	$P < 0.05$
		O. smaragdina	Moth (*C. suppressalis*)	10	2	3	$P < 0.05$
		T. melanocephala	Psyllid	14	3	6	$P < 0.01$
	Starved	*I. darwinanus*	Aphid	15	3	0	$P < 0.01$
		Campanotus	Brown plant hopper	12	3	1	$P < 0.05$
		Campanotus	Fly (*D. melanogaster*)	12	3	0	$P < 0.05$
Siler sp.	Well fed	*I. darwinanus*	Aphid	12	0	6	$P < 0.001$
		Campanotus	Brown plant hopper	10	2	0	$P < 0.05$
		S. geminata	Caterpillar	9	1	5	$P < 0.05$
		C. antarctica	Fly (*D. melanogaster*)	29	9	0	$P < 0.001$
		Campanotus	Fly (Notiphila)	15	6	1	$P < 0.05$
		T. melanocephala	Psyllid	7	0	4	$P < 0.01$
	Starved	*I. darwinanus*	Aphid	14	0	4	$P < 0.001$
		C. antarctica	Fly (*D. melanogaster*)	24	9	0	$P < 0.01$
Telamonia masinloc	Well fed	*C. antarctica*	Aphid	8	2	1	$P < 0.05$
		Campanotus	Brown plant hopper	14	3	0	$P < 0.01$
		Campanotus	Caterpillar (*C. medinalis*)	11	0	5	$P < 0.001$
		C. antarctica	Fly (*D. melanogaster*)	16	5	7	$P < 0.05$

TABLE IV continues

Salticid	Hunger state	Ant	Other insect	Ate ant	Ate other insect	Ate neither	Test of Goodness of fit
Telamonia masinloc	Well fed	*Campanotus*	Fly (Notiphila)	13	1	4	$P < 0.001$
		Pheidologeton	Green leaf hopper	19	6	1	$P < 0.01$
		Campanotus	Moth (*C. suppressalis*)	13	4	3	$P < 0.05$
		T. melanocephala	Psyllid	13	2	2	$P < 0.01$
	Starved	*C. antarctica*	Aphid	9	2	0	$P < 0.05$
		C. antarctica	Fly (*D. melanogaster*)	15	5	5	$P < 0.05$

TABLE V

Results from Type 3 tests (salticids given second prey while feeding on first) showing that ants were less often released to attack another insect than vice versa. All data from using living prey

Salticid	Hunger state	Ant	Other insect	Drops other insect to attack ant	Drops ant to attack other insect	Drops each to attack other	Drops neither	McNemar test
Euophrys sp. 1	Well fed	*I. darwinanus*	Aphid	16	2	0	24	$P < 0.001$
		T. melanocephala	Brown plant hopper	9	1	0	8	$P < 0.05$
		I. darwinanus	Fly (*D. melanogaster*)	16	2	0	24	$P < 0.001$
		T. melanocephala	Psyllid	13	2	1	15	$P < 0.01$
	Starved	*I. darwinanus*	Aphid	14	8	0	24	NS
		I. darwinanus	Fly (*D. melanogaster*)	14	6	0	26	NS
		T. melanocephala	Psyllid	25	9	0	21	$P < 0.01$
Euophrys sp. 2	Well fed	*I. darwinanus*	Aphid	9	1	0	7	$P < 0.05$
		T. melanocephala	Brown plant hopper	8	0	1	18	$P < 0.01$
		I. darwinanus	Fly (*D. melanogaster*)	8	1	0	6	$P < 0.05$
		T. melanocephala	Psyllid	9	0	0	10	$P < 0.005$
	Starved	*I. darwinanus*	Aphid	6	4	0	14	NS
		I. darwinanus	Fly (*D. melanogaster*)	8	3	0	10	NS
		T. melanocephala	Psyllid	13	3	0	16	$P < 0.05$
Chalcotropis sp.	Well fed	*I. darwinanus*	Aphid	10	2	0	17	$P < 0.05$
		T. melanocephala	Brown plant hopper	12	2	1	18	$P < 0.01$
		S. geminata	Caterpillar (*C. medinalis*)	7	0	0	10	$P < 0.01$

Salticid	Hunger state	Ant	Other insect	Drops other insect to attack ant	Drops ant to attack other insect	Drops each to attack other	Drops neither	McNemar test
Chalcotropis sp.	Well fed	*Campanotus*	Fly (Notiphila)	9	1	0	11	$P < 0.05$
		C. antarctica	Fly (*D. melanogaster*)	11	1	0	14	$P < 0.01$
	Starved	*I. darwinanus*	Aphid	11	6	0	14	NS
		Campanotus	Brown plant hopper	10	2	0	22	$P < 0.05$
		Campanotus	Fly (*D. melanogaster*)	10	5	0	15	NS
Siler sp.	Well fed	*I. darwinanus*	Aphid	5	0	0	9	$P < 0.05$
		Campanotus	Brown plant hopper	10	0	0	16	$P < 0.005$
		S. geminata	Caterpillar (*C. medinalis*)	7	0	0	12	$P < 0.01$
		C. antarctica	Fly (*D. melanogaster*)	8	1	0	6	$P < 0.05$
	Starved	*I. darwinanus*	Aphid	5	0	0	8	$P < 0.05$
		Campanotus	Brown plant hopper	5	0	0	13	$P < 0.05$
		C. antarctica	Fly (*D. melanogaster*)	7	1	0	5	$P < 0.05$
Telamonia masinloc	Well fed	*C. antarctica*	Aphid	7	1	0	3	$P < 0.05$
		Campanotus	Brown plant hopper	10	0	0	20	$P < 0.005$
		Campanotus	Caterpillar (*C. medinalis*)	7	0	0	12	$P < 0.01$
		C. antarctica	Fly (*D. melanogaster*)	6	0	0	5	$P < 0.05$
		Diacammon	Moth (*C. suppressalis*)	8	0	0	18	$P < 0.01$
	Starved	*C. antarctica*	Aphid	5	3	0	4	NS
		Campanotus	Brown plant hopper	7	0	0	12	$P < 0.01$
		C. antarctica	Fly (*D. melanogaster*)	7	3	0	4	NS

Discussion

Most salticids probably rarely, if ever, eat ants (Bristowe, 1941), but the five salticids considered in this chapter along with another 9 previously studied salticids (Edwards *et al.*, 1974; Cutler, 1980; Jackson & van Olphen, 1991, 1992; Chapter 2) appear to be exceptions to the rule. Ant-eating by these 14 species appears to be routine.

It may be tempting to call these 14 species 'ant-specialists' solely on the basis of their unusual diet. However, it is more informative to consider, step by step, and for each species, the four questions I raised in the introduction of the present chapter.

1) How do these species catch ants? More specifically, do they use prey-specific capture behaviour against ants? Apparently yes. Each of the five Philippines species tested, along with the 9 previously studied species, used one method for catching ants and a distinctively different method for catching other insects. *Euophrys* sp. 1 and 2 manoeuvred to attack ants head-on; *Siler* sp. routinely attacked ants from directly behind by stabbing and releasing until the ant became quiescent, then grasping the ant and holding on; *Chalcotropis* sp. and *Telamonia masinloc* attacked ants in rapid pursuits, but tended to orient head on; against ants, but not other prey, *Chalcotropis* sp. often attacked from ambush.

2) Do these species use prey-specific capture behaviour depending on whether prey is ant or another kind of insect? Apparently yes. If prey is an insect other than an ant, each of these five species tended to attack from just about any orientation and behaved similarly to how typical salticids are known to attack insects, but differently from how they attacked ants (Forster, 1977, 1982a).

3) How do the predatory strategies of these species compare to those of other ant-eating salticids? *Euophrys* sp. 1 and 2 from the Philippines resembled another two euophryines, *Corythalia canosa* (Jackson & van Olphen, 1991) and *Habrocestum pulex* from America (Chapter 2), by manoeuvring to attack ants head on. However, *Siler* sp. from the Philippines resembled the previously studied heliophanines (*Chrysilla lauta* and *Siler semiglaucous* from Sri Lanka, and

four species of *Natta* from Kenya: Jackson & van Olphen, 1992) by more often attacking from directly behind the ant. One of the euophryines, *Habrocestum pulex*, and all of the ant-eating heliophanines studied usually stabbed the ant one time before holding on. However, the other ant-eating euophryines studied, plus the one ant-eating plexippinine studied, usually attacked and held on. Among the euophryines, *Zendorus orbiculata* from Australia (Jackson & van Olphen, 1991) and *Chalcotropis* sp. from the Philippines differed from *Euophrys* sp. 1 and 2 from the Philippines and *Corythalia canosa* and *Habrocestum pulex* from America (Jackson & van Olphen, 1991; Chapter 2) by tending to attack ants from just about any orientation. However, *Chalcotropis* sp. and *Z. orbiculata* also differed from other ant-eating salticids by often attacking ants from ambush instead of actively pursuing them.

There appears to have been a tendency for pronounced predatory versatility to evolve in salticids that include unusual and dangerous prey in their diets (Jackson, 1992a): *Chalcotropis* sp., *Euophrys* sp. 1 and 2, *Siler* sp., and, to a lesser degree, *Telamonia masinloc*, along with araneophagic spartaeine salticids (Jackson, 1992b) and the previously studied ant-eating salticids (Jackson & Pollard, 1996), use different prey-capture tactics for different kinds of prey (*i.e.*, they have conditional predatory strategies).

Chalcotropis sp. and *Z. orbiculata* might be envisaged as having only moderately pronounced predatory versatility because they often caught ants and other insects in more or less the same way, but reserved ambush attacks for ants. However, in *Telamonia masinloc*, the only ant-eating plexippinine studied, predatory versatility is especially subtle: all prey were attacked in more or less the same way, with the only evident difference being a tendency to orient attacks more often head-on if the prey were an ant.

4) Do these species prefer ants to other insects? Apparently yes. Previous studies have suggested that, when salticids evolve prey-specific capture behaviour enabling them to be effective at catching unusual and dangerous prey not normally available to other salticids, there is a tendency for pronounced preferences for these unusual and dangerous prey to have evolved in these same salticids (Chapter 2, 4, and 5). In the present chapter, findings on

Chalcotropis sp., *Euophrys* sp. 1 and 2, and *Siler* sp. were consistent with this trend, as these four myrmicophagic species had both prey-specific capture behaviours and preferences for ants, and these prey-specific capture behaviours and preferences did not depend on prior experience with ants. *Telamonia masinloc* appears to demonstrate that preference for ants can evolve even when a myrmicophagic salticid has evolved only moderately pronounced prey-specific capture behaviour for this unusual prey.

After a 2-week period without food, *Telamonia masinloc* resembled *Corythalia canosa* and *Z. orbiculata* (Jackson & van Olphen, 1991) by appearing to take ants and aphids, and ants and flies, indiscriminately, but for other alternative prey there were distinct preference for ants. Also, in *Chalcotropis* sp., *Euophrys* sp. 1 and 2, and *Siler* sp., as in *Chrysilla lauta*, *Habrocestum pulex*, *Siler semiglaucous*, and *Natta* spp. (Jackson & van Olphen, 1992; Chapter 2), preference for ants was still pronounced after 2-week period without food. No explanation for this interspecific variation among species, and for variation among prey types in *Telamonia masinloc*, is apparent, but it may be that larger sample size tend to be necessary to show preference in started than in well-fed ant-eating salticids, and small sample size may account for the negative results in some instances.

5) Do the prey-specific capture behaviour and prey preference of these species depend on cues from different movement patterns of the different prey? Apparently no. As shown previously for *Habrocestum pulex* (Chapter 2), I provide evidence in the present study that, in five ant-eating salticid species from the Philippines, motionless lures are stalked and attacked, using the same prey-specific capture behaviours observed in tests with live, motile prey and also these five salticids show the same prey preference (for ants) observed in tests with live, motile prey. Apparently, prey movement is not necessary for these ant-eating salticids to distinguish ants from other insects.

SECTION III

ARANEOPHAGIC SALTICIDS

P56-61 -

This chapter as manuscript submitted to the Journal of insect Behavior 1995, has been acceptted and came out in October. Referees wanted to provide more information about prey-specific capture behaviour of spider-eating jumping spiders studied before.

CHAPTER 4

Prey preferences of *Portia fimbriata*, an araneophagic, web-building jumping spider (Araneae: Salticidae) from Queensland

Abstract: *Portia fimbriata* from Queensland, a previously studied jumping spider (Salticidae), routinely includes web-building spiders and cursorial salticids in its diet, both of these types of prey being dangerous and unusual prey for a salticid. The present paper is the first detailed study of *P. fimbriata*'s prey preferences. Three basic types of tests of prey preference were used, providing evidence that: 1) *P. fimbriata* males and females prefer spiders (both web-building spiders in webs and salticids away from webs) to insects; 2) *P. fimbriata* males and females prefer salticids to web-building spiders; 3) *P. fimbriata* males and females prefer larger spiders to smaller spiders; 4) there are intersexual differences in the preferences of P. fimbriata for prey size, females preferring larger prey and males preferring smaller prey; 5) *P. fimbriata*'s prey preferences are not affected by a prior period without food of two weeks. When preferences were tested for by using both living, active prey and dead, motionless lures, the same preferences were expressed, indicating that *P. fimbriata* can distinguish between different types of prey independent of the different movement patterns of different prey.

Introduction

'Specialization' is a term that has different meanings depending on whether it is applied to a predator's diet or its prey-capture behaviour (see Jackson & van Olphen, 1991, 1992). The diets of predators range from stenophagous to euryphagous. Stenophagous predators are commonly called 'specialists' with narrow, 'specialized' diets, but prey-capture behaviour is something different.

A stenophagous predator may or may not have evolved prey-specific ('specialized') capture behaviour for use against the few types of prey in its diet. Predators with 'prey-specific capture behaviours' are behaviourally 'specialized predators', and stenophagous predators may or may not be behaviourally specialized.

Euryphagous predators, on the other hand, are commonly called 'generalists' with 'unspecialized' diets. An euryphagous predator may use generalized ('unspecialized') capture behaviour against the numerous types of prey on which it normally feeds. Alternatively, an euryphagous predator may be 'versatile' (Curio, 1976): it might use a conditional predatory strategy consisting of a repertoire of disparate prey-specific capture behaviours, each for a different type of prey in its broad diet. In other words, a predator may have highly specialized prey-capture behaviour and yet be relatively unspecialized in diet.

Prey preference is another important behavioural trait of a predator, and it is distinct from a predator's diet and distinct from whether the predator has prey-specific capture behaviour. Preference, which implies ability to distinguish between different types of prey and choose to take one rather than the other, cannot be inferred simply from knowing the animal's diet in nature or from knowing the animal has prey-specific capture behaviour.

Spiders as a group are generally envisaged as relatively euryphagous (Bristowe, 1941; Foelix, 1982; Wise, 1993). However, scattered reports in the literature (for a brief review, see Nentwig, 1986) suggest that prey-specific capture behaviour and distinct preference for unusual prey may be surprisingly common in spiders. Among jumping spiders (Salticidae), there are two groups of species with especially pronounced predatory versatility - 'myrmicophagic salticids' (Edwards *et al.*, 1974; Cutler, 1980; Jackson & van Olphen, 1991, 1992) and 'araneophagic salticids' (Jackson & Blest, 1982a; Jackson & Hallas, 1986a; Jackson, 1992a).

The Salticidae is a large (*c.* 4000 described species) and diverse family (Prószyński, 1971; Coddington & Levi, 1991) with members on every continent (except Antarctica) and on most oceanic islands. These spiders are a major component of most terrestrial faunas and are one of the major animal groups in which acute vision has evolved (Land, 1974; Forster, 1982a; Blest & Carter, 1987; Blest *et al.*, 1990). It is not surprising that their highly developed vision is important during the pursuit and catching of prey (Heil, 1936; Drees, 1952; Forster, 1985), and acute vision may also make salticids especially likely to be selective foragers. Salticids have a pair of large anterior-medial eyes, known as

the principal eyes (Homann, 1928), and three pairs of smaller ("secondary") eyes responsible for movement detection (Land, 1971, 1974). The principal eyes are responsible for acute vision (Land, 1969a, b) and enable salticids, prior to contact, discriminate between different types of prey (Jackson & Blest, 1982b). Acute vision made possible by the salticid's principal eyes, creates the potential for pronounced preference behaviour.

In the ant-eating jumping spiders that have been studied in detail (Jackson & van Olphen, 1991, 1992), each individual uses a prey-specific capture behaviour for catching ants, an unusual and dangerous prey that most salticids do not normally take, and a different prey-specific behaviour for catching other insects. Also, in laboratory experiments, each of these species has been shown to have a distinct preference for ants over other types of insects (Jackson & van Olphen, 1991, 1992). Studies on ant-eating salticids suggest that, when predators evolve prey-specific capture behaviour for use against particularly dangerous and unusual prey of a type not generally available to other related predators, then they also tend to evolve distinct preference for these dangerous and unusual prey. However, a wider comparative base is needed for evaluating this hypothesis. Spider-eating (araneophagic) salticids (Jackson, 1992a), in common with the ant-eating salticids, have evolved prey-specific capture behaviour used against an unusual and dangerous prey, but the preferences of araneophagic salticids have not been tested rigorously.

Numerous salticids are known occasionally to leap or walk into webs and eat the resident spider (e.g., Robinson & Valerio, 1977), but only ten species of salticids (from 4 genera), all from the subfamily Spartaeinae (Wanless, 1984), are known to practise vibratory aggressive mimicry and the term 'araneophagic salticids' is restricted here to these species: *Brettus adonis*, *Brettus cingulatus* and *Gelotia lanka* from Sri Lanka; *Cyrba algerina* from southern Europe; *Cyrba ocellata* from Australia, Kenya, Sri Lanka and Thailand; five species of *Portia* (*P. africana* and *P. schultzi* from Kenya; *P. albimana* from Sri Lanka; *P. labiata* from Malaysia and Sri Lanka; and *P. fimbriata* from Australia, Malaysia and Sri Lanka) (Jackson & Hallas, 1986a, c; Jackson, 1990a, b).

After entering another spider's web, araneophagic salticids usually do not

simply stalk or chase down their victims but instead send vibratory signals across the silk (aggressive mimicry). The resident spider may respond to these signals in a way that is indistinguishable from how it would respond to a small insect ensnared in the web, but when the duped spider gets close, the araneophagic salticid lunges out and catches it. Each of these ten araneophagic salticids is also a versatile predator that catches prey outside webs by cursorial hunting, invades webs where it uses aggressive mimicry and catches the resident spider species and also takes insects and the resident spider's eggs from the alien web (Jackson, 1992a). However, no araneophagic salticids have been subjected to a detailed experimental study designed specifically to document preferences.

The habitat of one population of *Portia* - *P. fimbriata* in Queensland, Australia -is unique among those studied in having a superabundance of cursorial salticids (Jackson, 1988; Jackson & Blest, 1982a; Jackson & Hallas, 1986a) and apparently the Queensland *Portia* is, in its predatory behaviour, locally adapted to this locally abundant prey. *P. fimbriata* catches salticids by using a special type of trickery, 'cryptic stalking' (Jackson & Blest, 1982a), which capitalizes on *Portia*'s unusual appearance. Markings, tufts of hairs, and long, spindly legs give *Portia* the appearance of detritus in a web (Wanless, 1978, 1984), presumably affording it protection from visually hunting predators. Normally, locomotion is in a slow, choppy gait that renders *Portia* difficult to recognize even when moving. When inactive in a web, *Portia* adopts a special posture, the 'cryptic rest posture', with palps retracted to beside the chelicerae and legs retracted to beside and under the body, thereby blurring their outlines into the contours of the body (Jackson & Blest, 1982a).

When cryptically stalking a salticid, *P. fimbriata* moves even more slowly than usual, often going undetected until it is too late for the victim to escape. However, salticid secondary eyes being excellent movement detectors (Land, 1971), *P. fimbriata* sometimes has its victim suddenly swivelling around to see what is coming up on it. The Queensland *P. fimbriata* compensates: it freezes in its tracks and stays motionless until the salticid turns away again (Jackson & Blest, 1982a). When the salticid takes a look, it apparently perceives a piece of detritus. Another consistent component of cryptic stalking is that the Queensland

Portia retracts its palps, as in the cryptic rest posture. From experiments, it has been confirmed that hiding the outlines of palps is important for *Portia* because these outlines are cues by which the salticid can recognize the *Portia* as a predator (S.D. Pollard & R.R., Jackson, unpubl.data)

The Queensland *P. fimbriata*, by using distinctly different prey-capture behaviours depending on whether the prey is a web-building spider or a salticid, demonstrates that it perceives these as two distinctly different types of prey. Another salticid, because it can see well, is a special type of spider to take on as prey. However, whether Queensland *P. fimbriata* prefers salticids to other spiders as prey has not been investigated before.

Not only the taxonomic type of prey, but also size of prey may be important to *P. fimbriata*. Preferred size is not obvious. A larger prey may be advantageous because it provides a greater food pay off. However, a larger prey, especially if it is a spider, and perhaps even more so if it is a salticid, may be more likely than a smaller prey to injure or kill the *Portia*. Large meals appear to be more important for females than for males. Abdomens of gravid *P. fimbriata* females become very enlarged, but *P. fimbriata* males' abdomens vary little in size (Wanless, 1978). Perhaps, *P. fimbriata* females have a greater need for food and are accordingly more ready than males to take the risk entailed in pursuing larger prey. However, there have been on experimental comparisons of how *Portia*'s preferences vary with the size of the prey and with the sex of the *Portia*.

In some of the ant-eating salticids, preferences break down when the spider has been starved before the test (Jackson & van Olphen, 1991, 1992). That is, the starved ant eater appears ready to take prey indiscriminately, suggesting that preference is a luxury only a well-fed spider can afford. However, whether *Portia*'s preferences depend on hunger state is unknown.

Prey movement is an especially effective stimulus for eliciting orientation and pursuit by salticids (Drees, 1952; Dill, 1975) and for permitting salticids to distinguish between different types of prey (Freed, 1984). However, in a recent laboratory study (Jackson & Tarsitano, 1993), 11 salticid species, including four species of *Portia*, were tested and each stalked and attacked motionless lures. The four species of *Portia* appeared to be particularly effective at recognising

motionless lures in the laboratory study, and *Portia* is known readily to prey on quiescent web-building spiders in nature and in the laboratory (Jackson & Hallas, 1986a). However, whether *Portia*'s prey preferences depend on the different movement patterns of different prey has not been investigated.

In the present paper, I consider eight questions. 1) Does *P. fimbriata* prefer web-building spiders or insects as prey? 2) Does *P. fimbriata* prefer salticids or insects as prey? 3) Does *P. fimbriata* prefer salticids or web-building spiders as prey? 4) Does *P. fimbriata* prefer larger or smaller web-building spiders as prey? 5) Does *P. fimbriata* prefer larger or smaller salticids as prey? 6) How do the preferences of males and females compare? 7) Does hunger level affect *P. fimbriata*'s prey preference? 8) Do *P. fimbriata*'s preferences depend on cues from differences in the movement patterns of different prey?

Materials and methods

General

All tests were carried out in the laboratory using cultures of *Portia fimbriata* (adult male and female body length: *c.* 8 mm and 10 mm, respectively) started from spiders collected in Queensland. Species of spiders used as prey and lures (TABLE I) were collected either in Queensland or locally. The species from Queensland were from the same habitat as *P. fimbriata*, and *P. fimbriata* is known to feed on each of these spiders in nature (R. R. Jackson, unpubl. data). The insects used were from laboratory cultures. For any individual *P. fimbriata*, species of prey used for rearing were always different from species used in prey preference testing.

Laboratory maintenance procedures, cage design, basic testing methods and terminology were as in earlier salticid studies (Jackson & Hallas, 1986a; Jackson & van Olphen, 1991, 1992) and only essential details are given here. This included the convention that the expressions 'usually', 'sometimes', and 'occasionally' were used to indicate frequencies of occurrence of >80%, 20-80%, or <20%, respectively. The laboratory was on a 12L:12D light regime, with lights

TABLE I

Prey used in the laboratory for testing Queensland Portia fimbriata

Species	Description	Approximate body length (mm)	Used for rearing	Testing type	Origin
Achaearanea sp.	Web-building theridiid spider	5	Yes	Living prey	New Zealand
Badumna longinqua (L. Koch)	Web-building amaurobiid spider	10	Yes	Living prey	New Zealand
Tegenaria domestica (Clerck)	Web-building agelenid spider	5	Yes		New Zealand
Zosis geniculatus (Oliver)	Web-building uloborid spider	5	No	Living prey and lure	Queensland
Euophrys parvula Bryant	Cursorial salticid	7	Yes	Living prey	New Zealand
Jacksonoides queenslandica Wanless	Cursorial salticid	7	No	Living prey and lure	Queensland
Marpissa marina Goyen	Cursorial salticid	6	Yes		New Zealand
Trite planiceps (Urquhart)	Cursorial salticid	8	Yes		New Zealand
Lycosa sp.	Cursorial lycosid spider	7	Yes		New Zealand
Drosophila melanogaster (Meigen)	Fruit Fly	2	Yes	Living prey	Lab. culture
Musca domestica (Linnaeus)	House Fly	6	No	Living prey and lure	Lab. culture

coming on at 0800 hrs. Each test was carried out between 0900 hrs and 1700 hrs.

All *P. fimbriata* were fed only fruit flies prior to testing. 'Well-fed' and 'starved' *P. fimbriata* were kept without food for 7 and 14 days, respectively, prior to testing. Unless stated otherwise, all *P. fimbriata* were well fed.

Tests of prey preference using living prey

Tests with living prey were carried out using a prey preference testing box (PPTB) made from plastic consisting of ten 80 X 80 X 20 mm (length X width X height) cells. The top of the apparatus was transparent, but the sides of cells were opaque so that a *P. fimbriata* in one cell could not see into neighbouring cells. Each long side of the PPTB consisted of two pieces of plastic (an inner wall and an outer wall) 3 mm apart. Removable black cardboard screens fit between the inner wall and the outer wall. The apparatus had also two movable parts called 'comb'. Each comb consisted of ten 'teeth' (round wooden sticks 50 mm in length X 7 mm in diameter) extending from a plastic base. The ten teeth of the comb were positioned so that they could fit into the 10 plastic tubes (Fig. 1). Before testing began, one of the two tubes connected to each cell held a *P. fimbriata*; and the distal end of every tube was stoppered by the tips of the teeth of the comb. The second tube on each cell was empty before and during Type 1 & 2 tests. However, in Type 3 tests, the second tube contained a prey item that was a salticid or an insect but not a web-building spider (see below). To begin testing, the screens between the tubes and cells were removed and the two combs were pushed in slowly, forcing the ten *P. fimbriata* (and the 10 prey in Type 3 tests) into the cells. Once the *P. fimbriata* entered the cells, the screens were replaced.

Each test ended when the *P. fimbriata* captured a prey or 15 min elapsed, whichever came first, except that observations continued until the sequence ended if the *P. fimbriata* was in the act of pursuing a prey when the 15-min period elapsed. No individual *P. fimbriata* was used in more than one test of any one type. All *P. fimbriata* were fed only fruit flies prior to testing. 'Well-fed' and 'starved ' *P. fimbriata* were kept without prey for 5 and 15 days, respectively, prior

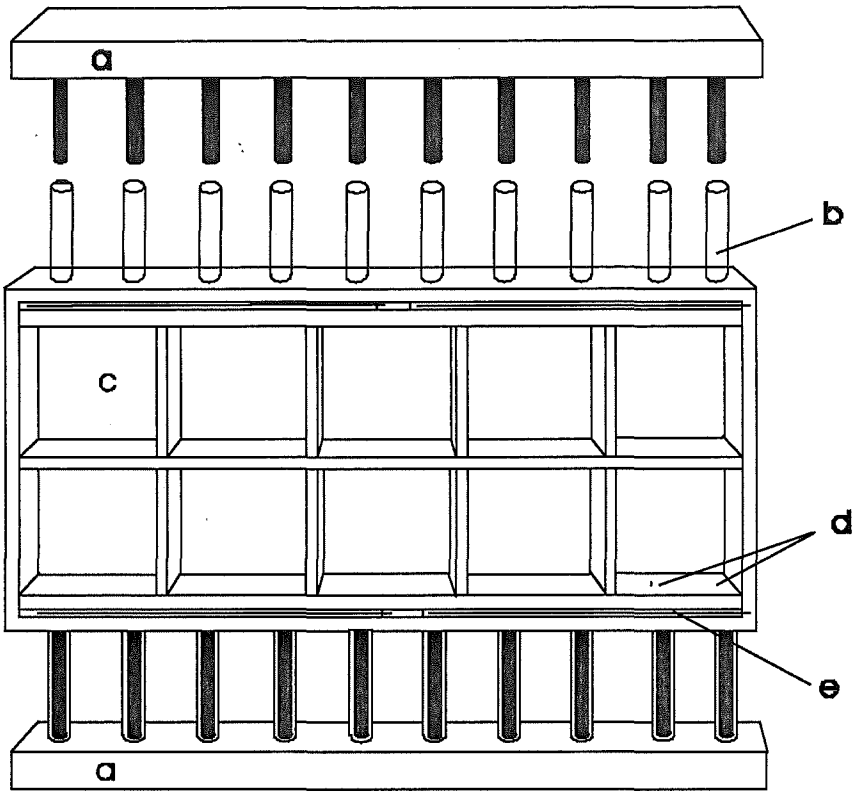

Fig. 1. Prey preference testing box (PPTB) used to test prey preferences of *Portia fimbriata* using living prey. a: comb with 10 teeth (round wooden sticks; black in diagram) that could be moved horizontally for pushing *P. fimbriata* into cells) - comb at top with teeth outside tubes; comb at bottom with teeth inside tubes); b: plastic tube; c: cell; d: 2 holes (diameter 8 mm) in the side of a cell; e: removable opaque cardboard screen. See text.

to testing.

Web spiders used as prey were in their own webs during tests, whereas salticids and insects used as prey were always away from webs. When using a web-building spider as prey, the web-building spider was put into a cell 3 days prior to a test and allowed to build a web.

Tests for the taxonomic category of prey preferred by well-fed P. fimbriata females

Web-building spiders, salticids and insects are referred to as the three "taxonomic categories of prey". Using these taxonomic categories of prey (web-building spider, salticid, and insect), three basic methods for testing preferences were used in these tests. These were, in basic respects, the same methods used previously in studies of ant-eating salticids (Jackson & van Olphen, 1991, 1992). Only 'small' prey (see below) and 'well-fed' (see above) *P. fimbriata* females were tested.

A. *Does P. fimbriata prefer web-building spiders or insects*?

1. *Type 1 tests (testing on alternate days with one type of prey at a time)*

Each *P. fimbriata* was used in a pair of tests (one type of prey on one day and the other type on the following day). Half of the *P. fimbriata* was tested first with web-building spiders; the other half was tested first with insects. Each *P. fimbriata* was assigned to one or the other of the two groups randomly.

2. *Type 2 tests (simultaneous testing with two prey)*

P. fimbriata was allowed to enter a cell containing one small web-building spider and one small insect to begin testing. The test ended when *P. fimbriata* took one of the two prey (*i. e.*, it was not allowed to take both).

3. *Type 3 tests (feeding P. fimbriata given an alternative prey)*

In one test, a *P. fimbriata* was given access to a web-building spider while feeding on an insect; in another test, the same *P. fimbriata* was given access to an insect while feeding on a web-building spider. Half of the *P. fimbriata* were

feeding on an insect first and half on a web-building spider first. Each *P. fimbriata* was assigned randomly to one or the other of the two groups. Normally, *P. fimbriata* spends more than an hour feeding on prey of the size used in the present study.

The first prey was put in a cell and a *P. fimbriata* was forced into the cell from the tube by pushing the teeth of the comb. After the *P. fimbriata* entered the cell, the hole was blocked. If *P. fimbriata* began eating the prey within 30 min, the second prey was introduced 15 min later by connecting another tube (containing the second prey) to the hole in the side of the cell. If the prey did not go into the cell within 60 s, it was pushed into the cell with comb.

In tests in which a *P. fimbriata* was given access to a web-building spider while feeding an insect or a salticid (see below), a 90-mm diameter cage made from a plastic petri-dish was used and an insect was put into the cage first and a *P. fimbriata* was allowed to enter the cage about 10 min later. The *P. fimbriata* was first placed in a transparent plastic tube (10 mm in diameter); within 5 min, one end of the tube was connected to a hole in the bottom of the cage and the other end was plugged with a cork. The *P. fimbriata* could enter the cage by walking up out of the tube and usually did so within 5 min. Once the *P. fimbriata* entered the cage, the tube was removed and the hole in cage was plugged with a cork. If the *P. fimbriata* began eating the insect within 30 min, the cover of cage with the feeding *P. fimbriata* on it, was removed *c.* 15 min later; next, this cage cover was placed on another open cage in which there was a web-building spider in its web.

If *P. fimbriata* did not capture and begin feeding on the first prey within the allowed 30 min, the test was attempted again on each succeeding day until it did so (maximum time that elapsed: 4 days).

B. *Does P. fimbriata prefer salticids or insects*?

Type 1 - 3 tests were carried out as described above, except that the two types of prey were salticids and insects, instead of web-building spiders and insects.

C. *Does P. fimbriata prefer salticids or web-building spiders*?

Type 1 - 3 tests were carried out as described above, except that the two types of prey were salticids and web-building spiders.

Tests for the size of prey preferred by well-fed P. fimbriata females

Three sizes of prey were recognized (see Jackson & Hallas, 1986a): very small (about one-tenth *P. fimbriata*'s estimated body volume), small (about half *P. fimbriata*'s estimated body volume), and large (about equal to *P. fimbriata*'s estimated body volume). Web-building spiders were in webs (see above), whereas salticids and insects were away from webs.

A. *Does P. fimbriata prefer larger or smaller web-building spiders*?

Using *P. fimbriata* females, Type 1 - 3 tests were carried out as described above except that, instead of using two taxonomic categories of prey, different sizes of one category (web-building spider) were used. Separate tests were carried out comparing preference for very small versus small, small versus large, and very small versus large web-building spiders.

In any given pair of tests (Type 1 or 3), both web-building spiders were either *Zosis geniculatus* or *Achaearanea* sp. In any single Type 2 test, the two prey were both either *Z. geniculatus* or both *Achaearanea* sp., and both individuals were, during the test, in the same web.

B. *Does P. fimbriata prefer larger or smaller salticids*?

These tests were the same as the tests for whether *P. fimbriata* prefers larger or smaller web-building spiders except that, instead of web-building spiders, salticids were used as prey.

C. *Does P. fimbriata prefer larger or smaller insects*?

These tests were the same as the tests for whether *P. fimbriata* prefers larger or smaller spiders, except that insects, instead of spiders, were used as prey and only two prey sizes were used: very small (*Drosophila melanogaster*, *c.* 2 mm in body length) and small (*Musca Domestica*, *c.* 6 mm in body length).

Large prey were not used because, in previous studies (Jackson and Blest, 1982; Jackson and Hallas, 1986a), *P. fimbriata* rarely took large insects.

Tests for the preferences of P. fimbriata males

All of the above tests carried out using *P. fimbriata* females were also carried out using *P. fimbriata* males. Results from testing with males were compared to results from testing with females.

Tests for the preferences of starved P. fimbriata females

All of the above tests carried out using well-fed *P. fimbriata* females were also carried out using starved *P. fimbriata* females, except that only small prey were used in these tests.

Tests of prey preference using motionless lures

P. fimbriata females were tested with motionless lures (Table I). The spiders used as lures (*Zosis geniculatus*, a web builder; *Jacksonoides queenslandica*, a salticid) were collected in Queensland from the same habitat as *P. fimbriata*, and *P. fimbriata* is known to prey on both of these species in nature (R. R. Jackson, unpubl. data). Insect lures were made from house flies. Each lure was made by killing the spider or fly by asphyxiation with carbon dioxide, then placing it in alcohol for 1 hr. After mounting the lure on the centre of one side of a disc-shaped piece of cork (diameter *c.* 1.25 times the body length of the animal), the lure plus the cork was sprayed with an aerosol plastic adhesive for preservation and for elimination of potential olfactory cues from the dead spider or fly. If *P. fimbriata* contacted the lure during a test, the lure was washed with 80% ethanol and allowed at least 24 h to dry before being used again.

Two types of choice ramp (CR) were used: Type I for when lures were away from webs and Type II for when lures were in the webs. Both types of CR were Y-shaped and made of wood. The Type I CR (Fig. 2) had two arms, each of which was 50 mm long and 40 mm wide, and a tail that was 50 mm long and 50 mm wide. The Type II CR (Fig. 3) had two arms, each of which was 105 mm

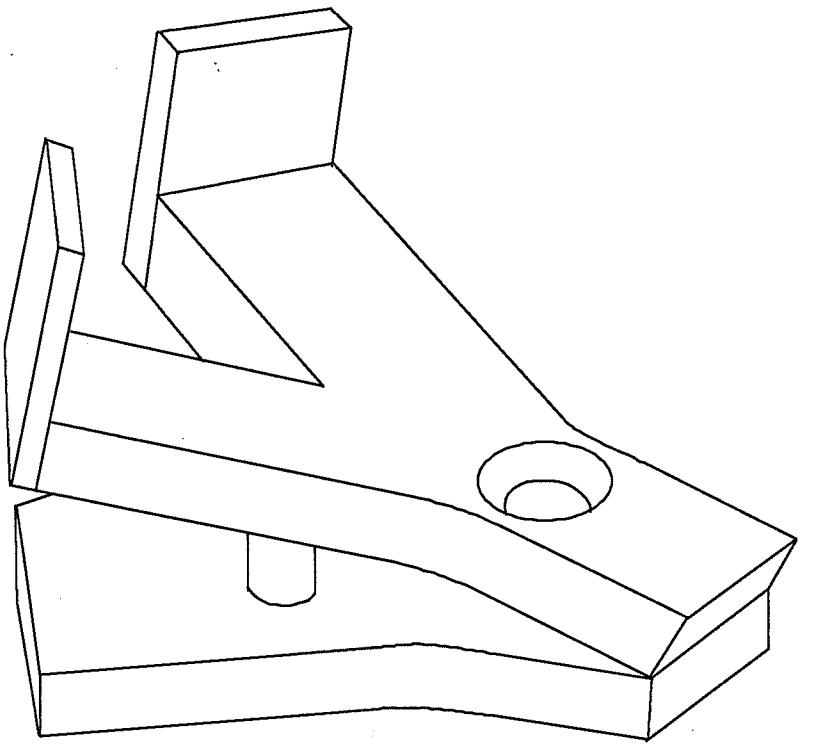

Fig. 2. Type I choice ramp (Type I CR) used to test prey preferences of *Portia fimbriata* using motionless lures that were away from webs. The pit was 30 mm in diameter (circle on right of diagram); the ramp consisted of two arms and two pieces of wood glued to the top of each arm. See text.

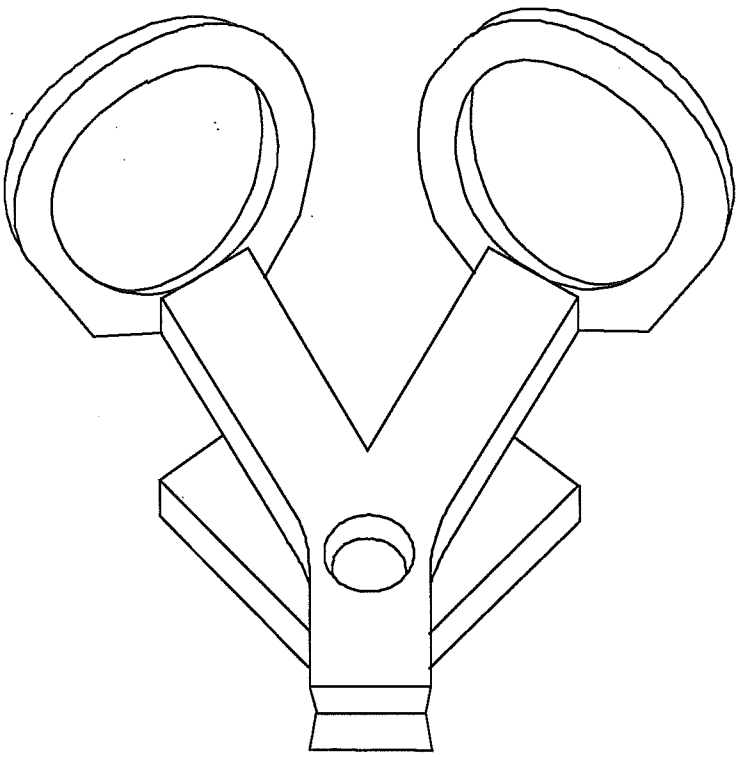

Fig. 3. Type II choice ramp (Type II CR) used to test prey preference of *P. fimbriata* using motionless lures that were in webs. The pit was 30 mm in diameter; the ramp consisted of two arms and two pieces of round wood (diameter 170 mm) glued to the top of each arm served as backgrounds against which *P. fimbriata* saw the lures and each held a plastic petri-dish contained a web. See text.

long and 40 mm wide, and a tail that was 50 mm long and 50 mm wide. The ramps were raised 20° from horizontal (Fig. 2 & 3), and each ramp was supported by a wooden pole that was 20 mm in diameter and glued to a wooden Y-shaped base. Ramps and bases were 15 mm and 12 mm thick, respectively. The pole was positioned on the base 90 mm from the far end of the tail. The entire apparatus were painted with two coats of water-resistant polyurethane. The ramp was wiped off with 80% ethanol, then allowed to dry for at least 30 min, between each test to remove possible chemical traces from any *P. fimbriata* that had been on the ramp in earlier tests.

The Type I CR had a rectangular piece of brown wood, 55 mm high and 40 mm wide, glued to the top end of each of the two arms at the ends of Y. These pieces of wood served as backgrounds against which *P. fimbriata* saw the lures.

The Type II CR had a round piece of brown wood (170 mm in diameter) glued to the top end of each of the two ramp arms. The round piece of wood served as a background against which *P. fimbriata* saw the prey on the web. In the round piece of wood, a hole was drilled (169 mm in diameter and 10 mm deep) that held a plastic petri dish (170 mm in diameter and 20 mm deep). The petri dish contained a web which had been built by a *Z. geniculatus*. Petri dishes were open during tests. For a lure, a web-building spider was glued to a cork disk and positioned at the centre of an otherwise vacant web. The disk stayed in place because webs of *Z. geniculatus* are very sticky. Vacant webs were obtained by removing the host spiders 7 days before tests began and leaving the webs exposed during this 7-day period.

At the start of tests in which lures were outside webs (i.e., *J. queenslandica* vs house fly and small *J. queenslandica* vs large *J. queenslandica*), we used the Type I CR and each lure was placed at the centre of an arm of the Y-shaped ramp. Each lure was positioned 10 mm above the base of the backing wood. To start a test in which either one or both of two types of lures was a web-building spider (i.e., *J. queenslandica* vs *Z. geniculatus*, *Z. geniculatus* vs house fly and small *Z. geniculatus* vs large *Z. geniculatus*), we used the Type II CR. When the lure was a *Z. geniculatus*, it was placed on the

web. When the lure was a *J. queenslandica* or a house fly, it was glued centred on the bottom of the petri dish. Each lure was positioned 40 mm above the base of the backing wood.

A 200 W incandescent lamp, positioned *c.* 400 mm overhead, lit the entire apparatus; fluorescent ceiling lamps provided additional (ambient) lighting. The apparatus was surrounded by a white cardboard screen on three sides, the open side being for the observer. The ramp was positioned so that, during the test, *P. fimbriata* moved away from the open side and the observer.

On the apparatus, there was a pit drilled through the ramp. The pit was 30 mm in diameter and centred 50 mm from the bottom end of the ramp tail. On the Type I CR, the pit was 70 mm from the lure. On the Type II CR, the pit was 150 mm from the lure. *P. fimbriata* can recognize prey of the size we used a distances of 2 - 3 X this far away (Jackson & Blest, 1982b). Lures were placed so that they faced 45° away from the pit. This was important because *P. fimbriata* generally will not approach a facing salticid (Jackson & Blest, 1982a).

Before starting a test, *P. fimbriata* was placed in the pit, and then the pit was covered with a clear plastic cover until *P. fimbriata* became quiescent. The cover was then removed to start the test. In a successful test, *P. fimbriata* walked slowly out of the pit and onto the ramp, then "scanned" its surroundings. A *P. fimbriata* "scanned" by standing in place while pivoting about and repeatedly fixating its principal eyes on objects in its environment. "Scanning", as defined here, should not be confused with Land's (1969b) use of this word for a specific movement pattern of the principal eye retinae.

The test was aborted if *P. fimbriata* stayed in the pit for as long as 30 min or moved off the ramp at the a line below where the two Y-shaped ramp arms joined. When tests were aborted, *P. fimbriata* was re-tested repeatedly, up to four times a day, then on subsequent days, until a successful test was completed or four days of unsuccessful testing elapsed.

P. fimbriata were chosen for tests at random from the laboratory cultures, and no individual *P. fimbriata* was used in more than one test of any one type. Successful tests ended when *P. fimbriata* did one of the following or 30 min elapsed after *P. fimbriata* left the pit: 1) arrived at an arm on which no prey lure

was present (applicable only to Type 1 tests, see below); 2) moved onto an arm and began to stalk the lure, but walked off the ramp arm before reaching the lure or the backing piece of wood; 3) moved onto an arm of a Type I CR, then leapt onto the backing piece of wood but did not attack the lure; 4) moved onto an arm of a Type II CR, then reached the base of the round wood that held petri dish but did not attack the lure; 5) arrived at an arm, stalked and approached the lure but did not attack it; 6) arrived at an arm, stalked while still distant, then retreated by walking backward and moved off the arm of the ramp; 7) arrived at an arm, then stalked and attacked the lure.

Only results 2 - 7 were taken as evidence of a choice. When using lures to test *P. fimbriata*'s preferences for different taxonomic categories of prey, lures were always "small" (see above). When testing for size preferences, lures were small vs large.

Terminology and the basics of testing procedure were as when living prey were used. The equivalent of Type 1 & 2 tests with living prey were carried out using lures, but the equivalent of Type 3 tests proved to be too difficult to do with lures. All tests were carried out using both well-fed and starved *P. fimbriata*.

Type 1 tests (testing on alternate days) with different taxonomic categories of lures

The categories were salticid spiders, web-building spiders, and house flies. In these tests, there was a lure on only one of the arms, and whether the lure was placed on the left or the right arm of the ramp was assigned randomly. Both well-fed and starved *P. fimbriata* were tested.

Type 1 tests (testing on alternate days) with different sizes of lures

In these tests, instead of using lures of different taxonomic categories, different sizes of the same species of prey were used as lures in each pair of tests.

Type 2 tests (simultaneous testing) with different categories of lures

In each trial, *P. fimbriata* was presented two types of lures, one on each

arm of the CR. If lures were salticids or house flies, the Type I CR was used. If one or both of the two lures was a web-building spider, the Type II CR was used.

Type 2 tests (simultaneous testing) with different sizes of lures

In these tests, instead of using lures of different taxonomic categories, the two lures were made from different sizes of the same species of prey. When presenting salticids or house flies, we used the Type I CR. When presenting web-building spiders, we used the Type II CR.

Analysis of data

When one prey or lure was presented at a time to *P. fimbriata* on alternate days (Type 1 tests), only those test-pairs in which *P. fimbriata* chose one prey or lure, but not the other, provided evidence of preference, and data were analyzed using McNemar tests for significance of changes. When two types of prey or lures were presented simultaneously to *P. fimbriata*, a series of tests in which one type of prey or lure was consistently chosen provided evidence of preference and tests for Goodness of Fit were used when analysing data. When a feeding *P. fimbriata* was given alternative prey (Type 3 tests), evidence of preference was provided only by those test-pairs in which the *P. fimbriata* dropped one prey to take the other in one, but not the other, of the two tests, and McNemar tests were used when analysing data (see Jackson & van Olphen, 1991; Sokal & Rohlf, 1981).

Pooling of data

There was no evidence that how often *P. fimbriata* chose one species of salticid, *J. queenslandica*, differed from how often *P. fimbriata* chose the other species of salticid, *E. parvula*. Therefore, all data from testing *P. fimbriata* with salticids, whether *J. queenslandica* or *E. parvula*, were pooled, and term "salticid(s)" was used for the pooled data set.

Also, there was no evidence that the particular species of web-building spider tested affected *P. fimbriata*'s preferences. Therefore, data from tests with *Zosis geniculatus* were pooled with data from tests with *Achaearanea* sp. and the

pooled data set was referred to simply as "web-building spider(s)".

Results

Tests for prey preference using living prey

Do well-fed P. fimbriata females prefer certain taxonomic categories of prey?

In tests on alternate days (Type 1 tests), when only a single prey type was presented at a time, *P. fimbriata* females ate web-building spiders and salticids more often than they ate insects; they also ate salticids more often than they ate web-building spiders (TABLE II).

In tests in which two prey were presented simultaneously (Type 2 tests), *P. fimbriata* females attacked web-building spiders and salticids first more often than they attacked insects first, and they attacked salticids first more often than they attacked web-building spiders first (TABLE III). In tests in which spiders were paired with insects, 26 out of 28 well-fed *P. fimbriata* females ate the web-building spiders they initially attacked and 27 out of 34 *P. fimbriata* females ate the salticids they initially attacked, but *P. fimbriata* females rarely attacked and ate insects. In tests in which web-building spiders in webs were paired with salticids away from webs, 25 out of 28 well-fed *P. fimbriata* females ate the salticids they initially attacked, and 12 out of 13 well-fed *P. fimbriata* females ate the web-building spider it initially attacked (TABLE IV).

In Type 3 test-pairs, when using web-building spiders and insects, *P. fimbriata* females never dropped the web-building spider to take the insect, but 11 well-fed *P. fimbriata* females dropped the insect to take the web-building spider (TABLE V). Also, when testing with salticids and insects, *P. fimbriata* females never dropped the salticid to take the insect, but 19 well-fed *P. fimbriata* females dropped the insect to take the salticid (TABLE V). However, in Type 3 tests in which feeding *P. fimbriata* were given alternative prey, when using salticids and web-building spiders, there were no significant differences in how often *P. fimbriata* females dropped web-building spiders to take salticids compared with how often they dropped salticids to take web-building spiders

TABLE II

Portia fimbriata tested on alternate days (Type 1 Tests)

	Ate prey 1 only	Ate prey 2 only	Ate both	Ate neither	McNemar test[3]
Web-building spider[1] (prey 1) vs fly[2] (prey 2)					
Well-fed *Portia fimbriata* female	19	0	0	7	$P < 0.0001$
Well-fed *Portia fimbriata* male	14	0	0	7	$P < 0.001$
Starved *Portia fimbriata* female	20	0	1	2	$P < 0.0001$
Salticid[2] (prey 1) vs fly[2] (prey 2)					
Well-fed *Portia fimbriata* female	45	0	0	17	$P < 0.0001$
Well-fed *Portia fimbriata* male	17	0	0	6	$P < 0.0005$
Starved *Portia fimbriata* female	32	1	1	12	$P < 0.0001$
Salticid[2] (prey 1) vs web-building spider[1] (prey 2)					
Well-fed *Portia fimbriata* female	19	5	16	11	$P < 0.01$
Well-fed *Portia fimbriata* male	14	2	12	6	$P < 0.01$
Starved *Portia fimbriata* female	20	6	16	4	$P < 0.01$

[1] In web

[2] Not in web

[3] Data in first two columns only used in these tests

TABLE III

Two prey presented to Portia fimbriata simultaneously (Type 2 tests)

	Attacked prey 1 first	Attacked prey 2 first	Attacked neither	Test of Goodness of fit[3]
Web-building spider[1] (prey 1) vs fly[2] (prey 2)				
Well-fed *Portia fimbriata* female	28	0	15	$P < 0.0001$
Well-fed *Portia fimbriata* male	18	0	8	$P < 0.0001$
Starved *Portia fimbriata* female	31	0	9	$P < 0.0001$
Salticid[2] (prey 1) vs fly[2] (prey 2)				
Well-fed *Portia fimbriata* female	34	0	13	$P < 0.0001$
Well-fed *Portia fimbriata* male	13	0	7	$P < 0.0001$
Starved *Portia fimbriata* female	41	0	5	$P < 0.0001$
Salticid[2] (prey 1) vs web-building spider[1] (prey 2)				
Well-fed *Portia fimbriata* female	28	13	5	$P < 0.05$
Well-fed *Portia fimbriata* male	16	5	7	$P < 0.05$
Starved *Portia fimbriata* female	26	12	4	$P < 0.05$

[1] In web

[2] Not in web

[3] Data in first two columns only used in these tests. Null hypothesis: if *Portia fimbriata* attacked a prey, P (prey attacked first was prey 1) = P (prey attacked first was prey 2)

TABLE IV

Two prey presented to Portia fimbriata simultaneously (Type 2 tests)

	Ate prey 1	Ate prey 2	Ate neither	Test of Goodness of fit[3]
Web-building spider[1] (prey 1) vs fly[2] (prey 2)				
Well-fed *Portia fimbriata* female	26	0	15	$P < 0.0001$
Well-fed *Portia fimbriata* male	17	0	8	$P < 0.0001$
Starved *Portia fimbriata* female	29	0	9	$P < 0.0001$
Salticid[2] (prey 1) vs fly[2] (prey 2)				
Well-fed *Portia fimbriata* female	27	0	13	$P < 0.0001$
Well-fed *Portia fimbriata* male	10	0	7	$P < 0.001$
Starved *Portia fimbriata* female	36	0	5	$P < 0.0001$
Salticid[2] (prey 1) vs web-building spider[1] (prey 2)				
Well-fed *Portia fimbriata* female	25	12	6	$P < 0.05$
Well-fed *Portia fimbriata* male	13	4	7	$P < 0.05$
Starved *Portia fimbriata* female	23	12	4	$P = 0.09$

[1] In web

[2] Not in web

[3] Data in first two columns only used in these tests. Null hypothesis: if *Portia fimbriata* ate a prey, P (prey eaten was prey 1) = P (prey eaten was prey 2)

TABLE V

Portia fimbriata given second prey while feeding on first prey (Type 3 tests)

	Drops prey 1 to attack prey 2	Drops prey 2 to attack prey 1	Drops each to attack other	Drops neither	McNemar test[3]
Web-building spider[1] (prey 1) vs fly[2] (prey 2)					
Well-fed *Portia fimbriata* female	0	11	0	31	$P < 0.001$
Well-fed *Portia fimbriata* male	0	8	0	24	$P < 0.01$
Starved *Portia fimbriata* female	0	13	0	23	$P < 0.001$
Salticid[2] (prey 1) vs fly[2] (prey 2)					
Well-fed *Portia fimbriata* female	0	19	0	12	$P < 0.0005$
Well-fed *Portia fimbriata* male	0	12	0	14	$P < 0.001$
Starved *Portia fimbriata* female	0	23	0	15	$P < 0.0001$
Salticid[2] (prey 1) vs web-building spider[1] (prey 2)					
Well-fed *Portia fimbriata* female	8	17	2	17	$P = 0.10$
Well-fed *Portia fimbriata* male	6	15	3	6	$P < 0.075$
Starved *Portia fimbriata* female	9	20	4	11	$P < 0.075$

[1] In web

[2] Not in web

[3] Data in first two columns only used in these tests

P80,1, 5 -

Yes. I defined three prey size in P67, par. 2. Very small prey are about one-tenth Portia's body volume, and small prey are about half Portia's body volume.

Do well-fed P. fimbriata females prefer certain size classes of prey?

P. fimbriata females in tests on alternate days (Type 1 tests), when only a single prey was presented at a time, ate small spiders (web builders and salticids) more often than very small spiders (both web-building spiders and salticids), and ate large spiders more often than they ate small spiders. However, *P. fimbriata* females ate very small and small insects at comparable rates (TABLE VI).

TABLE VI

Preference for certain sizes of prey.
Portia fimbriata tested on alternate days (Type 1 tests)

	Ate prey 1 only	Ate prey 2 only	Ate both	Ate neither	McNemar tests[3]
A. Prey: web-building spider[1]					
1. Well-fed *Portia fimbriata* female					
a. Very small (prey 1) vs small (prey 2)	2	13	0	13	$P < 0.05$
b. Small (prey 1) vs large (prey 2)	4	18	3	3	$P < 0.005$
c. Very small (prey 1) vs large (prey 2)	2	24	1	1	$P < 0.005$
2. Well-fed *Portia fimbriata* male					
a. Very small (prey 1) vs small (prey 2)	2	10	2	3	$P < 0.05$
b. Small (prey 1) vs large (prey 2)	8	1	0	7	$P < 0.05$
c. Very small (prey 1) vs large (prey 2)	3	3	0	10	NS
B. Prey: salticid[2]					
1. Well-fed *Portia fimbriata* female					
a. Very small (prey 1) vs small (prey 2)	0	18	0	17	$P < 0.0001$
b. Small prey (prey 1) vs large (prey 2)	6	24	5	0	$P < 0.005$
c. Very small (prey 1) vs large (prey 2)	0	27	4	4	$P < 0.0001$
2. Well-fed *Portia fimbriata* male					
a. Very small (prey 1) vs small (prey 2)	2	14	2	2	$P < 0.005$
b. Small (prey 1) vs large (prey 2)	13	2	0	3	$P < 0.005$
c. Very small (prey 1) vs large (prey 2)	5	1	1	11	NS
C. Prey: Insect[2]					
1. Well-fed *Portia fimbriata* female					
Very small (prey 1) vs small (prey 2)	0	0	0	35	NS
2. Well-fed *Portia fimbriata* male					
Very small (prey 1) vs small (prey 2)	0	0	0	18	NS

[1] In web

[2] Not in web

[3] Data in first two columns only used in these tests

P81,1, 5-6 -

In this part, I test preference for size classes of prey. The factor is prey size not taxonomic catologies of prey. In testing preference for taxonomic catologies of prey, I used three kinds of prey, web-spiders, salticids, and insect. In logical, in this part, I used different size classes of a single prey to see whether Portia prefers larger or small of a single prey. So, taxonomic catologies of prey are constant here, but size classes of prey are variable. The results (29/35) shows that Portia doesn't like insects at all. This is consistent with result of testing taxonomic prey.

In tests in which two prey of different sizes were presented simultaneously (Type 2 tests), *P. fimbriata* females ate small web-building spiders and salticids more often than they ate very small web-building spiders and salticids, and they ate large web-building spiders and salticids more often than small web-building spiders and salticids. However, there were no significant differences in how often *P. fimbriata* females ate very small insects and small insects (TABLE VII).

TABLE VII

Preference for certain sizes of prey: Portia fimbriata presented with two prey simultaneously (Type 2 tests). All P. fimbriata in these tests ate the prey attacked first. All P. fimbriata in these tests were well fed

	Attacked prey 1 first	Attacked prey 2 first	Attacked neither	Test of Goodness of fit[3]
A. Prey: web-building spider[1]				
1. Female				
a. Very small (prey 1) vs small (prey 2)	2	13	13	$P < 0.01$
b. Small (prey 1) vs large (prey 2)	5	17	6	$P < 0.01$
c. Very small (prey 1) vs large (prey 2)	2	17	9	$P < 0.001$
2. Male				
a. Very small (prey 1) vs small (prey 2)	3	12	2	$P < 0.05$
b. Small (prey 1) vs large (prey 2)	12	2	3	$P < 0.01$
c. Very small (prey 1) vs large (prey 2)	3	5	9	NS
B. Prey: Salticid[2]				
1. Female				
a. Very small (prey 1) vs small (prey 2)	1	17	17	$P < 0.0005$
b. Small (prey 1) vs large (prey 2)	7	21	7	$P < 0.01$
c. Very small (prey 1) vs large (prey 2)	1	24	10	$P < 0.0001$
2. Male				
a. Very small (prey 1) vs small (prey 2)	2	12	4	$P < 0.01$
b. Small (prey 1) vs large (prey 2)	13	1	4	$P < 0.001$
c. Very small (prey 1) vs Large (prey 2)	3	2	10	NS
C. Prey: Insect[2]				
1. Female				
Very small (prey 1) vs small (prey 2)	2	4	29	NS
2. Male				
Very small (prey 1) vs small (prey 2)	3	1	11	NS

[1] In web

[2] Not in web

[3] Data in first two columns only used in these tests

In tests in which *P. fimbriata* females were eating prey of one size when given access to another prey of the same species but a different size (Type 3 tests), it was more common for *P. fimbriata* females to drop very small web-building spiders and salticids to take small web-building spiders and salticids than to drop small spiders to take very small spiders. Also, *P. fimbriata* females dropped small spiders (both web-building spiders and salticids) to take large spiders more often than they dropped large spiders to take small spiders (TABLE VIII).

TABLE VIII

Preference for certain sizes of prey. Portia fimbriata given second prey while feeding on first prey (Type 3 tests). All P. fimbriata in these tests were well fed

	Drop prey 1 to attack prey 2	Drop prey 2 to attack prey 1	Drops each to attack other	Drops neither	McNemar test[3]
A. Prey: web-building spider[1]					
1. Female					
a. Very small (prey 1) vs small (prey 2)	10	3	0	15	$P < 0.05$
b. Small (prey 1) vs large (prey 2)	12	2	0	14	$P < 0.005$
c. Very small (prey 1) vs large (prey 1)	13	3	0	12	$P < 0.05$
2. Male					
a. Very small (prey 1) vs small (prey 2)	10	2	0	11	$P < 0.05$
b. Small (prey 1) vs large (prey 2)	3	11	0	8	$P < 0.05$
c. Very small (prey 1) vs large (prey 2)	4	2	0	16	NS
B. Prey: salticid[2]					
1. Female					
a. Very small (prey 1) vs small (prey 2)	12	1	0	22	$P < 0.005$
b. Small (prey 1) vs large (prey 2)	18	1	0	16	$P < 0.005$
c. Very small (prey 1) vs large (prey 2)	19	0	0	16	$P < 0.001$
2. Male					
a. Very small (prey 1) vs small (prey 2)	8	1	0	13	$P < 0.05$
b. Small (prey 1) vs large (prey 2)	2	9	0	11	$P < 0.05$
c. Very small (prey 1) vs Large (prey 2)	3	4	0	15	NS

[1] In web

[2] Not in web

[3] Data in first two columns only used in these tests

Do well-fed P. fimbriata males and females prefer the same prey?

In tests on alternate days (Type 1 tests), males resembled females of *P. fimbriata* by eating spiders (both web-building spiders and salticid spiders) more often than they ate similar size insects, and both males and females ate salticids more often than they ate similar size web-building spiders (TABLE II). In tests with simultaneously presented prey (Type 2 tests), males resembled females of *P. fimbriata* by attacking spiders first (both web-building spiders and salticids) more often than they attacked insects first, and both males and females attacked salticids first more often than they attacked web-building spiders first (Table III). In Type 2 tests in which spiders were paired with insects, 17 out of 18 well-fed *P. fimbriata* males ate the web-building spiders they initially attacked and 10 out of 13 well-fed *P. fimbriata* males ate the salticids they initially attacked, but no males attacked or ate any of the insects (TABLE III & IV). In tests in which web-building spiders were paired with salticids, 13 out of 16 well-fed *P. fimbriata* males ate the salticids they initially attacked, and 4 out of 5 male ate the web-building spider it initially attacked (TABLE III & IV). In Type 3 test-pairs, males resembled females of *P. fimbriata* by never dropping spiders, regardless of whether they were web-building spiders or salticids, to take insects, but both males and females sometimes dropped insects to take web-building spiders, and both males and females sometimes dropped insects to take salticids. However, there was no statistical evidence that males or females dropped web-building spiders to take salticids more often than they dropped salticids to take web-building spiders (TABLE V).

In tests on alternate days (Type 1 tests) using different sizes of prey, females consistently ate the relatively larger spiders (regardless of whether they were web-building spiders or salticids) more often than that ate the relatively smaller spiders, but males were different (TABLE VI). In common with females, males ate small spiders more often than they ate very small spiders. However, in contrast to females, males ate small spiders more often than they ate large spiders (TABLE VI).

In tests in which two sizes of prey were presented simultaneously (Type 2 tests), although females consistently ate the relatively larger spiders more often

than they ate the relatively smaller spiders (TABLE VII), males were different. Males resembled females by eating small spiders more often than they ate very small spiders, but they differed from females by eating small spiders more often they ate large spiders (TABLE VII).

In Type 1 and in Type 2 tests, there was no statistical evidence that males had a preference when tested with very small *vs* large spiders (TABLE VI and VII). Also, there was no statistical evidence of size preference when the prey was an insect in Type 1 tests or Type 2 tests (TABLE VI and VII). In fact, *P. fimbriata* never ate any of the insects, regardless of size, in Type 1 tests.

In tests in which a feeding *P. fimbriata* was given an alternative prey (Type 3 tests), it was more common for females to drop a relatively smaller spider (regardless of whether it was a web-building spider or a salticid) to take a relatively larger spider than to drop a relatively larger spider to take a relatively smaller spider, but males were different. It was more common for males to drop a relatively larger spider to take a relatively smaller spider than to drop a relatively smaller spider to take a relatively larger spider (TABLE VIII).

Tests for prey preference using motionless lures

Do well-fed P. fimbriata females prefer certain taxonomic categories of lures?

In tests on alternate days (Type 1 tests), when only a single lure was presented at a time, *P. fimbriata* females chose the spider lure, whether it be a salticid or a web-building spider, more often than they chose the insect lure (TABLE IX). Also, *P. fimbriata* females chose the lure made from a salticid spider more often than they chose the lure made from a web-building spider (TABLE IX). In tests with simultaneously presented lures (Type 2 tests), *P. fimbriata* females chose the spider (both web-building spider and salticid) lure more often than the insect lure, and they also chose the salticid lure more often than they chose the web-building spider lure (TABLE X).

TABLE IX

Portia fimbriata females tested on alternate days (Type 1 Tests) by using different taxonomic categories of motionless lures

	Chose prey 1 only	chose prey 2 only	chose both	chose neither	McNemar test[3]
Web-building spider[1] (prey 1) vs. fly[2] (prey 2)					
Well-fed *Portia fimbriata*	16	4	2	6	$P < 0.01$
Starved *Portia fimbriata*	18	5	2	3	$P < 0.01$
Salticid[2] (prey 1) vs. fly[2] (prey 2)					
Well-fed *Portia fimbriata*	21	2	2	3	$P < 0.001$
Starved *Portia fimbriata*	24	2	2	0	$P < 0.001$
Salticid[2] (prey 1) vs. web-building spider[1] (prey 2)					
Well-fed *Portia fimbriata*	13	3	5	7	$P < 0.05$
Starved *Portia fimbriata*	15	6	6	1	$P < 0.05$

[1] In web

[2] Not in web

[3] Data in first two columns only used in these tests

TABLE X

Two prey presented to Portia fimbriata simultaneously (Type 2 Tests).
Different taxonomic categories of motionless lures

	Chose prey 1 first	Chose prey 2 first	Chose neither	Test of Goodness of fit[3]
Web-building spider[1] (prey 1) vs. fly[2] (prey 2)				
Well-fed *Portia fimbriata*	17	5	6	$P < 0.01$
Starved *Portia fimbriata*	20	4	4	$P < 0.005$
Salticid[2] (prey 1) vs. fly[2] (prey 2)				
Well-fed *Portia fimbriata*	20	3	5	$P < 0.001$
Starved *Portia fimbriata*	24	4	0	$P < 0.001$
Salticid[2] (prey 1) vs web-building spider[1] (prey 2)				
Well-fed *Portia fimbriata*	15	6	7	$P < 0.05$
Starved *Portia fimbriata*	19	8	1	$P < 0.05$

[1] In web

[2] Not in web

[3] Data in first two columns only used in theses tests. Null hypothesis: if *Portia fimbriata* chose a prey, P (prey chosen was prey 1) = P (prey chosen was prey 2)

TABLE XI

Portia fimbriata tested on alternate days (Type 1 Tests) by using different size classes of motionless lures

	Chose prey 1 only	Chose prey 2 only	Chose both	Chose neither	McNemar test[3]
Large (prey 1) vs. small (prey 2) web-building spider[1]					
Well-fed *Portia fimbriata*	16	4	5	2	$P < 0.01$
Starved *Portia fimbriata*	19	4	4	1	$P < 0.005$
Large (prey 1) vs. small (prey 2) salticid[2]					
Well-fed *Portia fimbriata*	15	4	7	1	$P < 0.05$
Starved *Portia fimbriata*	17	5	6	0	$P < 0.05$

[1] In web

[2] Not in web

[3] Data in first two columns only used in these tests

TABLE XII

Two lures presented to Portia fimbriata simultaneously (Type 2 Tests). Different sizes of motionless lures

	Chose prey 1 first	Chose prey 2 first	Chose neither	Test of Goodness of fit[3]
Large (prey 1) vs. small (prey 2) web-building spider[1]				
Well-fed *Portia fimbriata*	15	5	8	$P < 0.05$
Starved *Portia fimbriata*	21	6	1	$P < 0.005$
Large (prey 1) vs. small (prey 2) salticid[2]				
Well-fed *Portia fimbriata*	19	5	4	$P < 0.005$
Starved *Portia fimbriata*	18	8	2	$P < 0.05$

[1] In web

[2] Not in web

[3] Data in first two columns only used in theses tests. Null hypothesis: if *Portia fimbriata* chose a prey, P (prey chosen was prey 1) = P (prey chosen was prey 2)

Do well-fed P. fimbriata females prefer certain size classes of lures?

In tests on alternate days (Type 1 tests), *P. fimbriata* females chose the lures made from large web-building spiders more often than they chose the lures made from small web-building spiders. Also, *P. fimbriata* females chose the lures made from large salticids more often than they chose the lures made from small salticids (TABLE XI). During tests in which two types of prey lures were presented simultaneously (Type 2 tests), *P. fimbriata* females chose the lures made from large web-building spiders more often than they chose the lures made from small web-building spiders. Also, *P. fimbriata* females chose the lures made from large salticids more often than they chose the lures made from small salticids (TABLE XII).

Details of P. fimbriata's behaviour during the tests with lures

When the pit was uncovered, *P. fimbriata* waved its palps up and down and eventually walked slowly out of onto the ramp. On the ramp, *P. fimbriata* scanned its surroundings by pausing for 2-3 s while facing in one direction, rotating 30-40° to face another direction, pausing again and so forth. After fixating its principal eyes on the lure one or more times, *P. fimbriata* usually headed towards it. When two types of lures were present, *P. fimbriata* usually fixated repeatedly on one lure then the other before finally moving toward one of the two.

When *P. fimbriata* moved toward a ramp arm on which a house fly lure or no lure was present, walking was at normal speed and in the normal posture. However, when a lure made from a salticid or a web-building spider was present, *P. fimbriata* adopted a slower walking gait. If the lure was a web-building spider, *P. fimbriata* might make vibratory signals on the web; if it was a salticid, *P. fimbriata* adopted the 'cryptic stalking' behaviour normally used against living salticids (Jackson & Blest, 1982a). When the lure was a spider (regardless of whether it was a web builder or a salticid), speed of approach steadily diminished as *P. fimbriata* neared it. However, insect lures and empty ramp arms were approached at more or less uniform speed.

When attacking a salticid lure, *P. fimbriata* usually picked it up without "lunging" at it or "swooping down" on it (see Jackson & Blest, 1982a). *P. fimbriata*

only occasionally leapt onto and never lunged onto a salticid lure. When the lure was a web-building spider positioned in a web, *P. fimbriata* never leapt onto the lure. Instead, *P. fimbriata* moved in a consistently slow fashion through the web and either simply picked the lure up or first lunged onto it. When the lure was an insect, *P. fimbriata* always attacked by picking it up without lunging at or swooping down on it.

If a lure was a large salticid, *P. fimbriata* sometimes retreated backwards, then approached again from about 20-30 mm away. When the lure was salticid of any size and *P. fimbriata* had stalked and reached a point at which it was facing the lure only *c.* 10-15 mm away, sometimes the *P. fimbriata* next made a circle, got behind the salticid lure, then attacked it from the rear.

Do starved and well-fed P. fimbriata prefer different prey?

In each type of test (Type 1 - 3), regardless of whether living prey or lures were used, well-fed and starved *P. fimbriata*'s preferences were similar (TABLE II - V, IX - XII).

Discussion

Taxonomic categories of prey preferred by P. fimbriata

Portia is a genus of salticids that has, for salticids, an unusual (*i. e.*, special) diet: in nature, all species of *Portia* studied feed frequently on web-building spiders (Jackson & Blest, 1982a; Jackson & Hallas, 1986a; Jackson, unpubl. data). Also, all species of *Portia* studied use prey-specific (*i. e.*, specialized) capture behaviour against web-building spiders (Jackson & Blest, 1982a; Jackson & Hallas, 1986a). In this chapter, I have illustrated yet another way in which the Queensland *P. fimbriata* is behaviourally specialized on spiders: *P. fimbriata* prefers spiders to insects. Ascertaining a predator's prey preference is distinct from knowing that a predator has an unusual diet and knowing that it has evolved prey-specific capture behaviour for a particular type of prey. However, the present study, plus earlier studies of ant-eating salticids (see

Jackson & van Olphen, 1991, 1992) suggest that specialisation in diet, prey-capture behaviour and preference vary together.

The Queensland *P. fimbriata* has, for *Portia*, an unusual (special) diet: the Queensland *P. fimbriata* frequently eats other species of salticids in nature (Jackson & Blest, 1982a). Also, the Queensland *P. fimbriata* uses a prey-specific (specialized) capture behaviour against the salticids on which it preys. Remarkably, in the present study, I found evidence that the Queensland *P. fimbriata* also prefers salticids to other spiders as prey. There appears to be a hierarchy of preferences: on a broader scale, Queensland *P. fimbriata* prefers both salticids and web-building spiders to insects as prey; on a finer scale, *P. fimbriata* prefers cursorial salticids over web-building spiders.

Earlier research on nine species of ant-eating salticids (Jackson & van Olphen, 1991, 1992) suggested that, in predators that take unusual and dangerous prey not normally available for other related predators, both prey-specific capture behaviour and distinctive preferences for these unusual and dangerous prey tend to evolve. In the present study, evidence from an araneophagic salticid provides support for this conclusion. Also, the present study suggests that the conclusion may apply even at a fine-scale level: the Queensland *P. fimbriata* has evidently evolved not only prey-specific capture behaviour for use against salticids but also the behaviour of preferring salticids to other spiders as prey.

The three basic types of tests used in the present study, and developed initially to test prey preferences of ant-eating salticids (Jackson & van Olphen, 1991), appear to be an especially effective way to test a predator's prey preferences. It would be interesting to apply these three basic types of tests in studies of other predators.

Males and females compared

In nature, males of all species of *Portia* studied frequently feed on the same types of web-building spiders as females (Jackson & Blest, 1982a; Jackson, unpubl. data). Also, males of all species of *Portia* studied use the same prey-specific capture behaviours against web-building spiders as females

(Jackson & Blest, 1982a; Jackson & Hallas, 1986a). In the present study, an additional similarity has been illustrated: both the males and the females of the Queensland *P. fimbriata* take web-building spiders in preference to insects as prey. Furthermore, males of the Queensland *P. fimbriata*, in common with females, frequently prey on cursorial salticids (Jackson & Blest, 1982a; Jackson, unpubl. data) and both males and females also use cryptic stalking (a specialized prey-catching behaviour) against cursorial salticids (Jackson & Hallas, 1986a). In the present study, I illustrated another similarity: both the males and the females of the Queensland *P. fimbriata* prefer cursorial salticids over web-building spiders as prey.

In all species of *Portia* studied, males tend to be less effective than females at catching both web-building spiders and insects; also, in the Queensland *P. fimbriata*, males tend to be less effective than females at catching cursorial salticids (Jackson & Hallas, 1986a). My results from the present study indicate that there is another intersexual difference: males prefer prey smaller than the prey preferred by females.

Similar intersexual variation is known for *Phidippus audax*, a common North American, and predominantly insectivorous, salticid: *P. audax* males tend to feed less often than females and, when they do feed, they tend to take smaller prey than females (Givens, 1978). Also, it has been suggested that similar intersexual differences may be widespread in the Salticidae (Jackson, 1982). In spiders, copulation is the male's only investment in the next generation, whereas females appear to have evolved a lifestyle that emphasizes the consumption of large quantities of food as an adaptation for producing yolk for eggs. Males, in contrast, appears to have evolved a lifestyle emphasizing courtship, mating, and searching for females (see Vollrath & Parker, 1992). Lesser emphasis by males of *P. fimbriata* on predation, in conjunction with preference for preying on smaller and therefore probably safer prey, appears to be consistent with this basic difference between male and female in lifestyle.

P. fimbriata's attack tactics when tested with motionless lures

In tests in which the prey were alive and motile, different types of prey

elicited different modes of stalking and different styles of attack consistent with behaviour seen in nature: when prey is a web-building spider in a web, *P. fimbriata* enters the web, uses aggressive mimicry, slowly stalks and attacks when close by lunging forward; when prey is a salticid away from webs, *P. fimbriata* cryptically stalks and attacks by swooping down on the prey; when prey is an insect outside webs, *P. fimbriata* normally stalks and attacks by simply picking the insect up. Before picking up prey, *P. fimbriata* usually first touches the prey with its forelegs, then slowly moves over and bites the prey. In contrast to most salticids, all species of *Portia* studied seldom leap on prey of any kind (Jackson & Blest, 1982a; Jackson & Hallas, 1986a).

In the present study, *P. fimbriata*'s behaviour when stalking and attacking lures was more or less consistent with *P. fimbriata*'s behaviour when prey was alive and except that picking up as an attack tactic was not reserved exclusively for insects. When tested with lures, *P. fimbriata* sometimes picked up not only insects but also spiders. This could be because, when close, *P. fimbriata* recognises that the lure is dead. That is, attacks on the lure are perhaps sometimes more accurately interpreted as scavenging behaviour, rather than predation. *P. fimbriata* sometimes encounters dead insects and spiders in webs in nature, and dead 'prey' is often picked up instead of being attacked by leaping, lunging or swooping down (Jackson & Hallas, 1986a). *Portia* may approach spider lures slowly and appropriately (*e.g.*, by cryptically stalking salticid lures) as a safe option until close enough to attack, by which time it may be certain the lure is dead.

Prey preferences of P. fimbriata in tests using motionless lures

In nature and in the laboratory, *P. fimbriata* readily preys on quiescent web-building spiders (Jackson & Blest, 1982a; Jackson & Hallas, 1986a). Under the controlled laboratory conditions in which a dead, motionless lure was used, apparently *P. fimbriata* not readily identified the lure as prey (also see Tarsitano & Jackson, 1992; Jackson & Tarsitano, 1993), but also as prey of a particular type. In the present study, when motionless lures made from different kinds of prey were used, *P. fimbriata* not only used the same prey-specific capture

behaviours that are typical of sequences in which prey are alive and active; *P. fimbriata* also expressed the same preferences as when prey are alive and motile. Evidently, in *P. fimbriata*, discrimination between types of prey does not depend on cues related to different types of prey moving differently.

Does hunger affect P. fimbriata's prey preferences

Hunger is shown to be an important internal factor that governs various facets of behaviours of predators (Curio, 1976), including salticids (Drees, 1952; Gardner, 1964). Little is known about how hunger effects the prey-preference behaviour of salticids. However, this has been investigated in the myrmicophagous salticids and found that, in *Chrysilla lauta, Corythalia canosa, Natta rufopicta,* other three species of *Natta*, *Pystira orbiculata*, and *Siler semiglaucus* (Jackson & van Olphen, 1991, 1992), well fed individuals had distinct preferences for ants, but these preferences broke down when these species had been starved for 2 weeks before tests. However, in the present study, I found no evidence that *P. fimbriata*'s preferences were affected by a prior period of 2 weeks without food comparable to that used in the study of ant-eating salticids. Why hunger level might affect the myrmicophagic and the araneophagic salticids differently is currently unclear.

CHAPTER 5

Prey preferences of *Portia africana*, *P. labiata* and *P. schultzi*, araneophagic, web-building jumping spiders (Araneae: Salticidae) from Kenya and Sri Lanka

Abstract: Prey-preference behaviour of three species of *Portia* (*P. africana*, *P. labiata* & *P. schultzi*), araneophagic jumping spiders (Salticidae) from Kenya and Sri Lanka, was studied in the laboratory for the first time by using prey preference tests previously used in studies of myrmicophagic salticids and in studies of another species of *Portia* (*Portia fimbriata* from Queensland). *P. africana*, *P. fimbriata*, *P. labiata* and *P. schultzi* routinely feed on web-building spiders, an unusual and potentially dangerous prey for a salticid. However, the Queensland *Portia fimbriata* uses cryptic stalking, a prey-specific capture behaviour, against cursorial salticids, a behaviour not known for any other species or population of *Portia*. Here I show that *P. africana* and *P. schultzi* from Kenya and *Portia labiata* from Sri Lanka resemble Queensland *Portia fimbriata* in having a pronounced preference for web-building spiders over insects. However, in contrast to Queensland *Portia fimbriata*, which preferred salticids to web-building spiders, *P. africana*, *P. labiata* and *P. schultzi* preferred web-building spiders to salticids. Similar to Queensland *Portia fimbriata*, female and male of *P. africana*, *P. labiata* & *P. schultzi* did not differ in their preferences for categories of prey, and their prey preferences did not vary in relation to hunger level. Also, the same preferences determined from tests using living, active prey were also found in tests using dead, motionless lures; evidently all four species of *Portia* can distinguish between different types of prey independent of their movement patterns.

Introduction

Predators are often described as relatively specialized or generalized, but these terms can refer to a number of different characteristics of the predator. This chapter, along with Chapter 2, 3 and 4 and a series of earlier papers (Jackson & van Olphen 1991, 1992), is a step toward understanding the different ways in which jumping spiders (Salticidae) may be specialized as predators.

Specialization may be considered in relation to diet: predators are more

or less stenophagous if they include only a narrow range of prey types (one or a few) in their diets and more or less euryphagous if they include a wide range of prey types in their diets. Specialization in prey-capture behaviour is different from diet (Morse, 1971, 1980; Fox & Morrow, 1981). For example, stenophagous predator may or may not have evolved 'specialized' (prey-specific) capture behaviour for use against the few types of prey in its diet. Also, a predator that is euryphagous in diet might be either 'specialized' or 'generalized' in prey-capture behaviour. That is, an euryphagous predator may use generalized (unspecialized) capture behaviour against the numerous types of prey on which it normally feeds. Alternatively, an euryphagous predator may be versatile' (Curio, 1976): it might use a conditional predatory strategy consisting of a repertoire of disparate prey-specific capture behaviours, each adaptively fine tuned to a different type of prey in its broad diet. A versatile predator is, therefore, euryphagous in diet but behaviourally a specialist on multiple prey types.

Prey preference is yet another way in which a predator may be specialized, and preference is distinct from both diet and prey-specific capture behaviour. That is, preference, which implies ability to distinguish between different types of prey and to choose to take one rather than the other, cannot be inferred simply from knowing the animal's diet in nature or knowing that the animal has prey-specific capture behaviour.

The Salticidae, a large family of spiders (Prószyński, 1971; Coddington & Levi, 1991) with unique, complex eyes and acute vision (Land, 1969a,b; 1974; 1985; Forster, 1982a; Blest *et al.*, 1990), may be a group in which selective foraging is especially likely: having acute vision, salticids can, prior to contact, discriminate between different types of prey (Jackson & Blest, 1982b).

Two groups of jumping spiders exhibit especially pronounced predatory versatility - ant-eating (myrmicophagic) species (Richman & Jackson, 1992; Chapter 2 & 3) and spider-eating (araneophagic) species (Jackson, 1992a).

The prey (ants and spiders) of myrmicophagic and araneophagic salticids are both unusual and potentially dangerous. Prey preferences of one species of araneophagic (Chapter 4) and 14 species of myrmicophagic (Jackson & van Olphen, 1991, 1992; Chapter 2 & 3) salticids have been studied in the laboratory

using a combination of three distinct testing methods. Each of the myrmicophagic species shows a preference for ants over other types of insects consistently across the three types of tests.

The most extreme known specialization on spiders as prey occurs in ten species of salticids (from 4 genera, *Brettus*, *Cyrba*, *Gelotia*, and *Portia*), all from the subfamily Spartaeinae (Wanless, 1984), and the term 'araneophagic salticids' is restricted in the present paper to these species (see Richman & Jackson, 1992). Each of these species also preys on insects, both in or out of webs.

In a web, the araneophagic salticid's strategy is usually not simply to stalk or chase down the resident spider, but instead to send deceptive vibratory signals across the silk (aggressive mimicry). The resident spider may respond to these signals in a way that appears indistinguishable from how it would respond to a small insect ensnared in the web, but when the duped spider gets close, the araneophagic salticid lunges out and catches it (Jackson, 1992a).

The most extensively studied araneophagic salticids are from the genus *Portia* (Jackson & Pollard, 1996) and, in particular, the species *P. fimbriata*. In *Portia*, behaviour repertoires vary among species and even among populations of single species. In particular, the habitat in which *P. fimbriata* lives in Queensland appears to be unique among those studied in having a superabundance of cursorial salticids (Jackson & Hallas, 1986a) and the Queensland *P. fimbriata* has a prey-specific capture for this locally abundant type of prey (Jackson, 1992b).

In Chapter 4, Queensland *P. fimbriata* was found to prefer web-building spiders to insects and salticids to other spiders as prey. Whether other *Portia* also prefer web-building spiders to insects has not been investigated before. Also, the earlier study left unresolved the question of whether a preference for salticids on web-building spiders is unique to the Queensland *P. fimbriata*, the only *Portia* known to have a prey-specific capture behaviour for this unique prey.

The present study is an attempt to clarify how other araneophagic salticids compare with the Queensland *P. fimbriata*.

In this chapter, the prey-preferences of *P. africana*, *P. labiata* and *P. schultzi* are investigated by considering the same six questions addressed in the

study of the Queensland *Portia fimbriata* (Chapter 4): 1) Does the predator prefer web-building spiders or insects as prey? 2) Does it prefer salticids or insects as prey? 3) Does it prefer web-building spiders or salticids as prey? 4) How do the preferences of males and females compare? 5) Does hunger level affect the predator's prey preference? 6) Do the predator's preferences depend on cues from different movement patterns of the different prey?

Materials and methods

General

Laboratory cultures of *P. africana* and *P. schultzi* originated from specimens collected in Kenya; those of *P. labiata* originated from Sri Lanka. Data presented here came from work on these cultures.

Each spider species used as prey and lures (TABLE I) was either collected from the field or derived from laboratory cultures. For any individual *Portia*, the species of prey used for rearing were always different from the species used in prey-preference testing.

Maintenance procedures, cage design, basic testing methods and terminology were as in earlier salticid studies (Jackson & Hallas 1986a; Jackson & van Olphen, 1991, 1992; Chapter 4), and only essential details are given here. Lights came on in the laboratory at 0800 h and went off at 2000 h. Each test was carried out between 0900 h and 1700 h.

All individual *Portia* were fed only fruit flies (*Drosophila melanogaster*) prior to testing. 'Well-fed' and 'starved' *Portia* were kept without food for 7 and 14 days, respectively, prior to testing. Unless stated otherwise, all *Portia* were well fed. All *Portia* tested were adults (body length: female, 8-10 mm; male, 6-7 mm). All prey and lures were about half the body size of the *Portia* ('small': see Chapter 4).

TABLE I

Prey used in the laboratory for testing Portia labiata from Sri Lanka, P. africana and P. schultzi from Kenya

Species	Description	*Portia* tested	Testing type	Origin
Achaearanea sp.	Web-building theridiid spider	*P. labiata*	Living prey	New Zealand
Badumna longinqua (L. Koch)	Web-building amarurobiid spider	*P. labiata*	Living prey	New Zealand
Ischnothele karschi (Bösenberg & Lenz)	Web-building diplurid spider	*P. africana* & *P. schultzi*	Living prey	Kenya
Zosis geniculatus (Oliver)	Web-building uloborid spider	All	Living prey and lure	Queensland & Kenya
Euophrys parvula Bryant	Salticid	*P. labiata*	Living prey	New Zealand
Jacksonoides queenslandica Wanless	Salticid	*P. labiata*	Living prey and lure	Queensland
Plexippus sp.	Salticid	*P. africana* & *P. schultzi*	Living prey and lure	Kenya
Menemerus sp.	Salticid	*P. africana* & *P. schultzi*	Living prey and lure	Kenya
Drosophila melanogaster (Meigen)	Fruit Fly	All	Living prey	Lab. Culture
Musca domestica (Linnaeus)	House Fly	All	Living prey and lure	Lab. Culture

Tests of prey preference using living prey

As in Chapter 4, tests with living prey were carried out in a prey preferences testing box made from plastic consisting ten cells (each cell 80 X 80 X 20 mm). The top of the apparatus was transparent, but the sides of each cell were opaque so that a *Portia* in one cell could not see into neighbouring cells. Before testing began, one of two tubes connected to each cell held a *Portia*; and the distal end of every tube was stoppered by the tips of the teeth of the 'comb'. The second tube on each cell was empty before and during Type 1 & 2 tests. However, in Type 3 tests, the second tube contained a prey item (a salticid or an insect, but not a web-building spider; see below). A prey item was put into each cell first and a *Portia* was allowed to enter the cell about 10 min later to begin the test. The *Portia* was first placed in one of the two tubes. To begin testing, screens between the tubes and cells were removed and the combs were pushed in slowly, forcing each of ten *Portia* (and 10 prey in Type 3 tests) into one of ten cells. Once the *Portia* entered the cells, the screens were replaced (for details, see Chapter 4).

The test ended when the *Portia* captured a prey or 30 min elapsed, whichever came first, except that observations continued until the sequence ended if the *Portia* was pursuing a prey when the 30-min period elapsed. No individual *Portia* was used in more than one test of any one type.

Salticids and insects used as prey were not associated with webs (no web present), whereas web spiders used as prey were always in their own webs during tests. Webs were built by web spiders, which were put into cells 3 days prior to a test.

Tests for prey preferences of well-fed Portia females

Three prey types (web-building spider, salticid, and insect) and three testing methods were used.

A. *Does Portia prefer web-building spiders or insects?*

1. *Type 1 tests (one individual of one prey type presented to a Portia at a time on alternate days)*

Each *Portia* was used in a pair of tests (one individual of one type of prey on one day and one individual of the other type on the following day). Half of the *Portia* was tested first with web-building spiders; the other half was tested first with insects. Each *Portia* was assigned to one of the two groups randomly.

2. *Type 2 tests (two types of prey presented to a Portia simultaneously; one individual prey of each type*)

Each test began when a *Portia* was allowed to enter a cell containing one web-building spider and one insect and ended when the *Portia* took one of the two prey (*i. e.*, it was not allowed to take both).

3. *Type 3 tests (Portia feeding on one prey type presented with alternative prey type*)

A *Portia* was given access to a web-building spider while feeding on an insect on one day; on the alternate day, the same *Portia* was given access to an insect while feeding on a web-building spider. Half of the *Portia* tested fed on an insect and half on a web-building spider in the first test (decided randomly).

The first prey was put in a cell and *Portia* was allowed to walk into the cell from the tube. After the *Portia* entered the cell, the hole was blocked. If the *Portia* began eating the prey within 60 min, the second prey was introduced 30 min later by connecting another tube (containing the second prey) to the hole in the side of the cell. If the prey did not go into the cell within 60 s, it was pushed into the cage with a brush. The test ended when the *Portia* either dropped the first prey to take the second or ignored the second prey and kept feeding for 30 min.

In tests in which a *Portia* was given access to a web-building spider while feeding an insect or a salticid (see below), a 90-mm-diameter cage made from a plastic petri dish was used and an insect was put into the cage first and a *Portia* was allowed to enter the cage about 10 min later. The *Portia* was first placed in a transparent plastic tube (10 mm in diameter); within 5 min, one end of the tube was connected to a hole in the bottom of the cage and the other end was plugged with a cork. The *Portia* could enter the cage by walking up out of the tube and usually did so within 5 min. Once the *Portia* entered the cage, the

tube was removed and the hole in the cage was plugged with a cork. If the *Portia* began eating the insect within 30 min, the cover of the cage with the feeding *Portia* on it, was removed *c.* 15 min later; next, this cage cover was placed on another open cage in which there was a web-building spider in its web.

If *Portia* did not capture and begin feeding on the first prey within the allowed 60 min, the test repeated on each succeeding day until it did so; maximum time that elapsed: 4 days).

B. *Does Portia prefer salticids or insects*?

Type 1, Type 2, and Type 3 Tests were carried out as described above, except that the two types of prey were salticids and insects, instead of web-building spiders and insects.

C. *Does Portia prefer salticids or web-building spiders*?

Type 1, Type 2, and Type 3 tests were carried out as described above, except that the two types of prey were salticids and web-building spiders, instead of web-building spiders and insects.

Tests for the preferences of well-fed Portia males and for the preferences of starved Portia females and males

All the above tests on well-fed *Portia* females were also carried out on well-fed *Portia* males. Results from testing males were compared with results from testing females.

All of the above tests carried out on well-fed *Portia* females were also carried out using starved *P. labiata* males and females and starved *P. africana* and *P. schultzi* females.

Tests of prey preference using motionless lures

Each lure was mounted on a cork and the lure plus cork was sprayed with an aerosol plastic adhesive for preservation and for elimination of potential odour cues from the dead spider or fly (see Chapter 4). If *Portia* contacted the lure during a test, the lure was washed with 80% ethanol and allowed at least 24h to

dry before being using again.

Two types of choice ramp (CR) were used (see Chapter 4): Type I when lures were away from webs and Type II when lures were in webs. The ramp was wiped off with 80% ethanol, then allowed to dry for at least 30 min, between each test to remove possible chemical traces from *Portia* that had been on the ramp in earlier tests.

The Type I CR had two arms backed by vertical blank walls at the ends of the Y. Lures was located in front of the walls. The Type II CR was also a Y, but each arm ended at a wall holding a plastic petri dish containing a *Zosis geniculatus* web. Petri dishes were open during tests. For a lure, a web-building spider was glued to a cork disk and positioned at the centre of an otherwise vacant web. The disk stayed in place because webs of *Zosis geniculatus* are very sticky. Vacant webs were obtained by removing the host spiders 7 days before tests began and leaving the webs exposed during this 7-day period. (For details, see Chapter 4).

For tests in which lures were outside webs (*i.e.*, salticid vs fly), the Type I CR was used. For tests in which one of two types of lures was a web-building spider (*i.e.*, salticid vs *Zosis geniculatus*, fly vs *Zosis geniculatus*), the Type II CR was used. When the lure was a *Zosis geniculatus*, it was placed on the web at the centre of the petri dish. When the lure was a salticid or a house fly, it was glued to the centre of the petri dish. Each lure was positioned 40 mm above the base of the cardboard.

Before starting a test, the *Portia* was placed in the pit, and the pit was then covered with a clear plastic cover until the *Portia* became quiescent. The cover was then removed to start the test.

The test was aborted if *Portia* stayed in the pit for 30 min or moved off the ramp to the line below where the two arms of the Y-shaped ramp joined. When tests were aborted, *Portia* was re-tested repeatedly, up to four times a day, then on subsequent days, until a successful test was completed or four days of unsuccessful testing elapsed.

Portia were chosen for tests at random from the laboratory cultures, and no individual *Portia* was used in more than one test of any one type. Successful

tests ended when *Portia* did one of the following or 30 min elapsed after *Portia* left the pit: 1) arrived at an arm on which no lure was present (applicable only to Type 1 tests, see below); 2) moved onto an arm and began to stalk the lure, but walked off the ramp arm before reaching the end; 3) moved onto an arm of the Type I CR, then leapt off without attacking the lure; 4) moved onto an arm of the Type II CR, then reached the end but did not attack the lure; 5) arrived at an arm, stalked and approached the lure, but did not attack it; 6) arrived at an arm, stalked while still distant, then retreated by walking backward and moving off the arm of the ramp; 7) arrived at an arm, then stalked and attacked the lure. Only results 2 - 7 were taken as evidence of a choice.

Terminology and the basics of testing procedure for dead prey were as when living prey were used. The equivalent of Type 1 & 2 tests with living prey were carried out using lures, but the equivalent Type 3 tests proved too difficult to perform with lures. All tests were carried out using both well-fed and starved *Portia*.

Type 1 testing (testing on alternate days) with different categories of lures

Each individual *Portia* was used in a pair of tests (one type of lure on one day and the other type on the following day). Half of the *Portia* were tested first with one type of lure; the other half were tested first with the other type of lure (*Portia* assigned to the 2 groups randomly). In these tests, only one of the Y ramp arms had a lure present; the other one was without a lure. Whether the lure was placed on the left or the right arm of the ramp was assigned randomly.

Type 2 testing (simultaneous testing) with different categories of lures

In each trial, a *Portia* was tested with two types of lures. If lures were salticids or house flies, the Type I CR was used and one type of lure was placed at the end of each arm of the ramp. If one (or both) of the two lures was a web-building spider, the Type II CR was used for testing. Lures made from web-building spiders were placed in the web in the centre of the petri dish. If the lure was made from a salticid or a house fly, it was glued onto the centre of a petri dish in which there was no web.

Data presentation

Since there was no evidence that the particular species of web-building spider tested affected *Portia*'s preferences, data from tests with were pooled and pooled data sets were referred to as simply 'web-building spiders'. Also, since *Portia*'s choice of one species of salticids did not appear to differ from how it chose other species of salticids, data from testing *Portia* with different species of salticids were pooled and referred to as simply as 'salticids'.

Results

Tests for prey preference using living prey

In tests on alternate days (Type 1 tests), when only a single prey type was presented at a time, *P. africana*, *P. labiata* and *P. schultzi* males and females attacked and ate web-building spiders more often than they attacked and ate flies; they also ate web-building spiders more often than they ate salticids (TABLE II).

Males and females of each species of *Portia* attacked salticids more often than they attacked insects (TABLE II). However, *Portia* often attacked, released, then re-attacked salticids. Because of this, salticids that were attacked often were not eaten before the time allotted for the tests ended and, in some instances, there was no statistically significant difference in how often *Portia* ate salticids and insects.

In tests in which two prey were presented simultaneously (Type 2 Tests), *P. africana*, *P. labiata* and *P. schultzi* males and females attacked and ate web-building spiders first more often than they attacked flies first (TABLE III). Males and females of each species attacked salticids more often than they attacked flies, and they ate web-building spiders in these tests more often than they ate salticids. As in Type 1 Tests, *Portia* tended to attack, release and re-attack salticids, and often salticids attacked were not eaten in the time allotted for tests. The data suggested a trend to attack web-building spiders first more often than they attacked salticids first, but this was, in most instances (exceptions: well-fed

TABLE II

Portia tested on alternate days (Type 1 Tests)

	Attacked (ate) prey 1 only	Attacked (ate) prey 2 only	Attacked (ate) both	Attacked (ate) neither	McNemar test[1]
Web-building spider[2] (prey 1) vs fly[3] (prey 2)					
Well-fed *P. labiata* female	27 (24)	4 (4)	9 (8)	4 (8)	$P<0.0005$ ($P<0.0005$)
Well-fed *P. labiata* male	17 (16)	2 (2)	4 (3)	10 (12)	$P<0.005$ ($P<0.005$)
Starved *P. labiata* female	18 (15)	3 (3)	7 (4)	2 (8)	$P<0.005$ ($P<0.005$)
Starved *P. labiata* male	15 (15)	3 (3)	6 (4)	2 (4)	$P<0.00$ ($P<0.005$)
Well-fed *P. schultzi* female	23 (23)	5 (4)	8 (6)	5 (8)	$P<0.005$ ($P<0.0005$)
Well-fed *P. schultzi* male	20 (14)	6 (5)	5 (3)	5 (14)	$P<0.01$ ($P<0.05$)
Starved *P. schultzi* female	18 (18)	5 (4)	5 (5)	2 (3)	$P<0.01$ ($P<0.005$)
Well-fed *P. africana* female	24 (22)	3 (3)	10 (6)	3 (9)	$P<0.0005$ ($P<0.0005$)
Well-fed *P. africana* male	21 (13)	3 (4)	8 (3)	5 (17)	$P<0.0005$ ($P<0.05$)
Starved *P. africana* female	18 (17)	4 (4)	5 (5)	2 (13)	$P<0.005$ ($P<0.005$)
Salticid[3] (prey 1) vs fly (prey 2)					
Well-fed *P. labiata* female	25 (22)	5 (5)	9 (8)	8 (12)	$P<0.0005$ ($P<0.005$)
Well-fed *P. labiata* male	18 (8)	7 (7)	3 (3)	7 (17)	$P<0.025$ (NS)
Starved *P. labiata* female	24 (18)	6 (6)	11 (10)	4 (11)	$P<0.005$ ($P<0.025$)
Starved *P. labiata* male	16 (9)	6 (5)	8 (6)	4 (14)	$P<0.05$ (NS)
Well-fed *P. schultzi* female	19 (15)	4 (4)	10 (7)	3 (10)	$P<0.005$ ($P<0.025$)
Well-fed *P. schultzi* male	17 (7)	5 (5)	7 (3)	5 (19)	$P<0.01$ (NS)
Starved *P. schultzi* female	16 (10)	4 (2)	4 (3)	3 (12)	$P<0.01$ ($P<0.025$)
Well-fed *P. africana* female	27 (18)	7 (5)	11 (7)	4 (19)	$P<0.005$ ($P<0.025$)
Well-fed *P. africana* male	24 (14)	8 (10)	5 (1)	5 (17)	$P<0.005$ (NS)
Starved *P. africana* female	20 (15)	6 (7)	8 (5)	4 (11)	$P<0.01$ (NS)
Salticid (prey 1) vs web-building spider (prey 2)					
Well-fed *P. labiata* female	2 (1)	15 (14)	16 (15)	4 (7)	$P<0.005$ ($P<0.005$)
Well-fed *P. labiata* male	2 (1)	13 (12)	5 (4)	10 (13)	$P<0.005$ ($P<0.005$)
Starved *P. labiata* female	3 (2)	16 (14)	18 (15)	2 (8)	$P<0.005$ ($P<0.005$)
Starved *P. labiata* male	2 (1)	12 (12)	5 (4)	8 (10)	$P<0.01$ ($P<0.005$)
Well-fed *P. schultzi* female	1 (0)	9 (10)	4 (1)	7 (10)	$P<0.025$ ($P<0.005$)
Well-fed *P. schultzi* male	2 (1)	12 (11)	15 (14)	2 (5)	$P<0.01$ ($P<0.005$)
Starved *P. schultzi* female	1 (1)	9 (9)	4 (4)	5 (5)	$P<0.025$ ($P<0.025$)
Well-fed *P. africana* female	4 (1)	16 (16)	17 (14)	2 (8)	$P<0.01$ ($P<0.0005$)
Well-fed *P. africana* male	1 (1)	11 (12)	6 (2)	6 (9)	$P<0.005$ ($P<0.005$)
Starved *P. africana* female	0 (1)	9 (11)	12 (8)	7 (8)	$P<0.005$ ($P<0.005$)

[1] Data in first two columns only used in these tests

[2] In web

[3] Outside web

TABLE III

Two prey presented to Portia simultaneously (Type 2 tests)

	Attacked prey 1 first (ate prey 1)	Attacked prey 2 first (ate prey 2)	Attacked neither (ate neither)	Test of Goodness of fit[1]
Web-building spider[2] (prey 1) vs fly[3] (prey 2)				
Well-fed *P. labiata* female	26 (25)	5 (5)	8 (9)	$P<0.0005$ ($P<0.0005$)
Well-fed *P. labiata* male	18 (16)	3 (3)	7 (9)	$P<0.005$ ($P<0.005$)
Starved *P. labiata* female	25 (25)	9 (8)	1 (2)	$P<0.01$ ($P<0.005$)
Starved *P. labiata* male	20 (19)	5 (4)	6 (8)	$P<0.005$ ($P<0.005$)
Well-fed *P. schultzi* female	20 (18)	4 (4)	4 (6)	$P<0.005$ ($P<0.005$)
Well-fed *P. schultzi* male	15 (14)	2 (2)	6 (7)	$P<0.005$ ($P<0.005$)
Starved *P. schultzi* female	19 (19)	7 (6)	2 (3)	$P<0.025$ ($P<0.01$)
Well-fed *P. africana* female	19 (18)	0 (1)	9 (9)	$P<0.0001$ ($P<0.0001$)
Well-fed *P. africana* male	15 (14)	3 (2)	6 (8)	$P<0.005$ ($P<0.005$)
Starved *P. africana* female	24 (23)	6 (4)	3 (6)	$P<0.005$ ($P<0.005$)
Salticid[3] (prey 1) vs fly (prey 2)				
Well-fed *P. labiata* female	24 (14)	11 (10)	5 (16)	$P<0.05$ (NS)
Well-fed *P. labiata* male	19 (10)	7 (5)	10 (21)	$P<0.025$ (NS)
Starved *P. labiata* female	19 (11)	8 (8)	4 (12)	$P<0.05$ (NS)
Starved *P. labiata* male	19 (12)	8 (5)	3 (13)	$P<0.05$ (NS)
Well-fed *P. schultzi* female	16 (10)	6 (6)	4 (10)	$P<0.05$ (NS)
Well-fed *P. schultzi* male	16 (8)	6 (4)	6 (16)	$P<0.05$ (NS)
Starved *P. schultzi* female	15 (9)	5 (5)	3 (9)	$P<0.025$ (NS)
Well-fed *P. africana* female	22 (6)	8 (9)	1 (16)	$P<0.01$ (NS)
Well-fed *P. africana* male	17 (4)	7 (8)	5 (17)	$P<0.01$ (NS)
Starved *P. africana* female	24 (10)	11 (12)	1 (14)	$P<0.05$ (NS)
Salticid (prey 1) vs web-building spider (prey 2)				
Well-fed *P. labiata* female	13 (2)	20 (20)	12 (23)	NS ($P<0.0005$)
Well-fed *P. labiata* male	10 (1)	19 (17)	9 (20)	NS ($P<0.0005$)
Starved *P. labiata* female	15 (4)	27 (25)	6 (19)	NS ($P<0.0005$)
Starved *P. labiata* male	10 (2)	19 (17)	10 (20)	NS ($P<0.005$)
Well-fed *P. schultzi* female	10 (5)	16 (15)	9 (15)	NS ($P<0.025$)
Well-fed *P. schultzi* male	13 (4)	14 (14)	5 (14)	NS ($P<0.025$)
Starved *P. schultzi* female	12 (8)	20 (19)	4 (9)	NS ($P<0.025$)
Well-fed *P. africana* female	6 (3)	19 (19)	9 (12)	$P<0.01$ ($P<0.005$)
Well-fed *P. africana* male	6 (2)	12 (11)	14 (19)	NS ($P<0.01$)
Starved *P. africana* female	9 (4)	20 (22)	2 (5)	$P<0.05$ ($P<0.005$)

[1] Data in first two columns only used in these tests

[2] In web

[3] Outside web

TABLE IV

Portia given second prey while feeding on first prey (Type 3 tests)

	Drop prey 1 to attack prey 2	Drop prey 2 to attack prey 1	Drops each to attack other	Drops neither	McNemar test[1]
Web-building spider[2] (prey 1) vs fly[3] (prey 2)					
Well-fed *P. labiata* female	2	16	0	18	$P < 0.005$
Well-fed *P. labiata* male	1	10	0	12	$P < 0.01$
Starved *P. labiata* female	2	17	0	15	$P < 0.005$
Starved *P. labiata* male	1	11	0	9	$P < 0.005$
Well-fed *P. schultzi* female	1	13	0	14	$P < 0.005$
Well-fed *P. schultzi* male	1	8	0	10	$P < 0.005$
Starved *P. schultzi* female	0	10	1	12	$P < 0.005$
Well-fed *P. africana* female	1	13	0	14	$P < 0.005$
Well-fed *P. africana* male	2	10	0	10	$P < 0.025$
Starved *P. africana* female	0	8	0	18	$P < 0.01$
Salticid[3] (prey 1) vs fly (prey 2)					
Well-fed *P. labiata* female	5	4	0	22	NS
Well-fed *P. labiata* male	4	5	0	12	NS
Starved *P. labiata* female	6	4	0	19	NS
Starved *P. labiata* male	4	6	0	18	NS
Well-fed *P. schultzi* female	5	4	0	22	NS
Well-fed *P. schultzi* male	4	5	0	12	NS
Starved *P. schultzi* female	2	5	0	19	NS
Well-fed *P. africana* female	5	4	0	22	NS
Well-fed *P. africana* male	4	5	0	12	NS
Starved *P. africana* female	0	3	1	17	NS
Salticid (prey 1) vs web-building spider (prey 2)					
Well-fed *P. labiata* female	15	2	2	15	$P < 0.005$
Well-fed *P. labiata* male	11	1	3	11	$P < 0.005$
Starved *P. labiata* female	14	2	4	15	$P < 0.005$
Starved *P. labiata* male	10	2	1	12	$P < 0.025$
Well-fed *P. schultzi* female	13	2	2	12	$P < 0.005$
Well-fed *P. schultzi* male	10	1	3	8	$P < 0.025$
Starved *P. schultzi* female	7	0	0	20	$P < 0.025$
Well-fed *P. africana* female	13	3	2	12	$P < 0.025$
Well-fed *P. africana* male	10	2	3	8	$P < 0.025$
Starved *P. africana* female	7	0	0	19	$P < 0.025$

[1] Data in first two columns only used in these tests

[2] In web

[3] Outside web

and starved *P. africana* females), not significant. Some of the attacks on salticids may have been, in the close quarters of the test apparatus, more accurately interpreted as defensive (attempts to drive the salticid away) rather than predatory; this may account for some, if not all, of the non-significant data sets.

When using web-building spiders and flies in Type 3 tests, all three species of *Portia* dropped flies to take web-building spiders more often than they dropped web-building spiders to take the flies (TABLE VI). They also dropped salticids to take web-building spiders more often than they dropped web-building spiders to take salticids. However, when using salticids and flies as pairs, how often *Portia* females dropped flies to take salticids did not differ statistically from how often they dropped salticids to take flies (TABLE VI).

Tests for prey preference using motionless lures

In tests on alternate days (Type 1 Tests), when only a single lure was presented at a time, *P. africana*, *P. labiata* and *P. schultzi* chose lures made from web-building spiders more often than they chose lures made from flies. Also, each species chose lures made from web-building spiders more often than they chose lures made from salticids. *P. africana* and *P. schultzi* chose lures made from salticids more often than they chose lures made from flies. There was no statistically significant difference in how often lures made from salticids and lures made from flies were chosen by either well-fed or starved *P. labiata* (TABLE V). Pooling data for well-fed and starved *P. labiata*, there was a significant ($P<0.05$) trend to choose salticids over flies. Well fed *P. africana* and *P. schultzi* females chose lures made from salticids more often than they chose lures made from flies.

In tests with simultaneously presented lures (Type 2 tests), *P. africana*, *P. labiata* and *P. schultzi* chose web-building spider lures more often than insect lures and also chose web-building spider lures more often than they chose salticid lures. There was no statistically significant difference in how often lures made from salticids and lures made from flies were chosen by *P. africana*, *P. labiata* and *P. schultzi* (TABLE VI); however, pooled data from all three species was significant ($P<0.01$).

Do starved and well-fed Portia prefer different prey?

In each type of test, both males and females of well-fed *Portia* of each species and starved *Portia* of each species exhibited similar preferences.

TABLE V

Portia tested on alternate days (Type 1 Tests) by using different categories of motionless lures

	Chose lure 1 only	chose lure 2 only	chose both	chose neither	McNemar test[1]
Web-building spider[2] (lure 1) vs. fly[3] (lure 2)					
Well-fed *P. labiata* female	17	5	4	5	$P < 0.01$
Starved *P. labiata* female	16	6	4	3	$P < 0.05$
Well-fed *P. schultzi* female	17	5	6	10	$P < 0.01$
Well-fed *P. africana* female	20	3	4	11	$P < 0.005$
Salticids[3] (lure 1) vs. fly (lure 2)					
Well-fed *P. labiata* female	12	6	4	9	NS
Starved *P. labiata* female	15	8	5	1	NS
Well-fed *P. schultzi* female	16	6	4	15	$P < 0.05$
Well-fed *P. africana* female	16	6	4	13	$P < 0.05$
Salticids (lure 1) vs. web-building spider (lure 2)					
Well-fed *P. labiata* female	4	14	7	6	$P < 0.025$
Starved *P. labiata* female	6	15	8	0	$P < 0.05$
Well-fed *P. schultzi* female	4	14	7	11	$P < 0.025$
Well-fed *P. africana* female	2	13	7	9	$P < 0.005$

[1] Data in first two columns only used in these tests

[2] In web

[3] Outside web

TABLE VI

Two prey presented to Portia simultaneously (Type 2 Tests), different categories of motionless lures

	Chose lure 1 first	Chose lure 2 first	Chose neither	Test of Goodness of fit[1]
Web-building spider[2] (lure 1) vs. fly[3] (lure 2)				
Well-fed *P. labiata* female	17	6	8	$P < 0.025$
Starved *P. labiata* female	16	5	4	$P < 0.025$
Well-fed *P. schultzi* female	17	7	8	$P < 0.05$
Well-fed *P. africana* female	20	8	12	$P < 0.025$
Salticids[3] (lure 1) vs. fly (lure 2)				
Well-fed *P. labiata* female	14	8	9	NS
Starved *P. labiata* female	15	9	5	NS
Well-fed *P. schultzi* female	19	11	13	NS
Well-fed *P. africana* female	19	10	10	NS
Salticids (lure 1) vs web-building spider (lure 2)				
Well-fed *P. labiata* female	5	17	8	$P < 0.01$
Starved *P. labiata* female	5	16	8	$P < 0.025$
Well-fed *P. schultzi* female	4	12	10	$P < 0.05$
Well-fed *P. africana* female	8	19	9	$P < 0.05$

[1] Data in first two columns only used in theses tests

[2] In web

[3] Outside web

Discussion

It appears that *P. africana* and *P. schultzi* from Kenya and *P. labiata* from Sri Lanka have, in common with *Portia fimbriata* from Queensland (Chapter 4), a preference for web-building spiders over insects: consistently, across Type 1 - 3 tests, for all species of *Portia* studied, males and females chose web-building spiders over insects. Preference for web-building spiders over insects may be general to this genus and, perhaps, to other araneophagic spartaeine salticids (*Brettus*, *Cocalus*, *Cyrba* & *Gelotia*), although further comparative studies would be useful for validating this point. The present paper, along with the earlier studies on the Queensland *P. fimbriata* (Chapter 4) and on myrmicophagic salticids (Jackson & van Olphen, 1991, 1992; Chapter 2 & 3), suggests that there has been a tendency for predators that have evolved prey-specific capture behaviour for use against unusual and dangerous prey, normally unavailable for other related predators, also to have evolved distinctive preferences for these prey. Why this might be so is not obvious.

There appears to be an interesting parallel in how prey preference and prey-specific capture behaviour differ among the species of *Portia* studied. The Queensland *P. fimbriata*, but not the other *Portia* studied, uses a salticid-specific capture behaviour (Jackson & Hallas, 1986a), and consistently, across Type 1 - 3 tests, the Queensland *P. fimbriata* prefers salticids to web-building spiders. However, *P. africana*, *P. labiata* and *P. schultzi* consistently ate web-building spiders in preference to salticids. Salticids are especially common in *P. fimbriata*'s habitat in Queensland, and it appears that local abundance of cursorial salticids has shaped the evolution of, not only salticid-specific capture behaviour, but also prey-preference behaviour.

The Queensland *P. fimbriata* consistently, across all types of tests, preferred salticids to flies. Preference for salticids over flies does not appear to be so strongly expressed in *P. africana*, *P. labiata* and *P. schultzi*; males and females of each of these species attacked salticids more often than they attacked flies in Type 1 and 2 tests, but there was no evidence of preference in Type 3

tests. Type 3 tests, where the criterion for preference comes from the predator dropping one prey to take another, might be envisaged as a test for stronger preference than Type 1 and 2 tests.

Influences of hunger on the behaviour of predators (Curio, 1976), including salticids (Drees, 1952; Gardner, 1964) and other spiders (Punzo, 1989), are well known, but whether hunger affects the prey-preferences of salticids has received little attention prior to recent studies of myrmicophagic salticids: in *Corythalia canosa*, *Chrysilla lauta*, *Natta* spp. and *Siler semiglaucus* (Jackson & van Olphen, 1991, 1992), well-fed individuals prefer ants to other prey, but individuals of these species, when starved for 2 weeks prior to testing, appear to take prey indiscriminately. For *C. canosa*, *C. lauta*, *Natta* spp. and *S. semiglaucus*, preference may be a luxury affordable only by a well-fed individual. However, in *Habrocestum pulex* (Chapter 2), another myrmicophagic salticid, and in araneophagic *Portia fimbriata* from Queensland (Chapter 4), there is no evidence that a prior period of 2 weeks without food affects prey preferences. Data from the this study indicate that *P. africana*, *P. labiata* and *P. schultzi* resemble Queensland *Portia fimbriata*: a two-week period without food had no noticeable effect on preferences. It is currently unclear why the relation between hunger and preference differs among the salticid species studied.

Prey movement is an especially effective in stimulating salticids to orient and pursue prey (Drees, 1952; Dill, 1975). Also, different styles of movement may sometimes be cues by which salticids distinguish between different types of prey (Freed, 1984). However, movement is not always necessary. Numerous species of salticids occasionally stalk and attack motionless prey (Forster, 1985; Jackson & Tarsitano, 1993), and the species of *Portia* studied appear to be unusual in that they routinely prey on quiescent web-building spiders (Jackson & Hallas, 1986a). On the basis of visual cues alone, *Portia* can distinguish between quiescent spiders, insects and eggsacs (Jackson, 1995). *Portia* uses against different kinds of motionless prey the prey-specific capture behaviour they normally use against the same kinds of living prey (Jackson & Tarsitano, 1993). Furthermore, in Chapter 4 when tested using dead, motionless prey, the Queensland *P. fimbriata* showed the same preferences as in tests using living prey. In this study, *P.*

africana, *P. labiata* and *P. schultzi* had the same preferences when tested with dead, motionless lures as when tested with living, motile prey. Evidently, cues from prey shape alone are sufficient both for eliciting prey-specific capture behaviour and for the expression of prey-preference in salticids.

SECTION IV

FINE TUNING OF PREFERENCE IN RELATION TO RISK

CHAPTER 6

The biology of *Scytodes* sp. indet., a spitting spider (Araneae: Scytodidae) from Los Banos: silk utilisation, maternal, social and predatory behaviour

Abstract: The biology of *Scytodes* sp. indet, a rainforest spitting spider (Scytodidae) from Los Banos in the Philippines, was studied in both the field and the laboratory. *Scytodes* lives in a web built on large leaves (green and living or dead, dry and brown). The web is a sparsely woven sheet across a concave upper leaf surface, with a three-dimensional, tubular nest linked to the sheet via one small opening. *Scytodes* is a versatile predator that captures prey either in webs or cursorially (away from webs), and prey capture may be either by ambush or by active pursuit regardless of whether in the presence and absence of webs. Other spiders, especially jumping spiders (Salticidae), appear to be *Scytodes*' dominant prey. *Scytodes* avoided beetles, bees, wasps and ants; it also avoided *Myrmarachne* sp., ant-like jumping spiders. Females carry their eggsacs by their chelicerae until the eggs hatch. Mother-offspring associations are prolonged, with juveniles tending not to depart from their mother's web until after the third moult. Females provision their young with food (parental care) by dragging prey back to in the nest. Predatory sequences usually include tapping, spitting, stabbing, wrapping and feeding, with large prey being spat at and stabbed repeatedly.

Introduction

Scytodes, a genus of about a half dozen tropical and subtropical spider species in the family Scytodidae (Bristowe, 1958; Brignoli, 1976; Alayón, 1977; Valerio, 1981), is unique among spiders in predatory behaviour because, from their chelicerae, these spiders spit a sticky gum over their prey (Monterosso, 1928; Millot, 1930; Bristowe, 1931, 1958; Dabelow, 1958; McAlister, 1960; Gestsch, 1979; Gilbert & Rayor, 1985). Spitting behaviour is absent in the other scytodid genera, *Loxosceles* (Gertsch, 1967) and *Drymusa* (Valerio, 1974). Few details are available concerning the prey of *Scytodes* in nature, but Nentwig's

(1985) study of *Scytodes longipes* Lucas is particularly interesting because, in addition to catching insects, this species tends especially often to include other spiders in its diet. Spiders in the genus *Scytodes* are also of interest because *S. intricata* Banks from Panama practises maternal care of egg sacs and young (Eberhard, 1986) and because *S. fusca* Walckenaer from Queensland lives in colonies and has at least rudimentary social behaviour (Bowden & Jackson, 1988).

The present paper is the first report on the predatory, maternal and social behaviour of *Scytodes* sp. indet. from Los Banos in the Philippines, an araneophagic scytodid with pronounced predatory versatility. The systematics of Asian *Scytodes* is poorly known, and the distinctive *Scytodes* reported on in the present paper is probably a new, undescribed species. The legs and body of *Scytodes* sp. indet. are pale yellow with black markings. All legs are thin, and legs I are especially long. Chelicerae are small with short fangs. The abdomen and cephalothorax are dorso-ventrally elevated. For convenience, this spider will be referred to simply as '*Scytodes*'. Voucher specimens have been deposited at the Florida State Collection of Arthropods, Division of Plant Industry, Florida, USA.

Materials and methods

General

The field site was tropical rain forest and agricultural plots near and in Los Banos in south Luzon, the Philippines. For laboratory studies, *Scytodes* was maintained and tested in vertical wood-frame cages (120 X 120 X 50 mm) with removable glass sides (see Fig. 1 in Jackson & Wilcox, 1993a) and cages made from plastic petri dishes (90 mm in diameter) in rooms with controlled light (12L:12D), temperature (*c.* 25°C) and relative humidity (*c.* 80%). Laboratory studies were carried out on 200 juveniles (*c.* 2 - 6 mm in body length) and adults (body lengths: females, *c.* 8 mm; males, *c.* 6 mm). These included both laboratory-reared and field-collected individuals; as there was no evidence that

origin affected behaviour, data from laboratory-reared and field-collected individuals were pooled. Maintenance, data analysis, and testing procedures followed earlier studies (see Jackson & Hallas, 1986a) and only the details specific this study are described below.

Definitions of phasing, amplitude, duration and site of movement are illustrated with the following example. When two legs or palps wave (dorso-ventrally) at the same time, they are considered to be in 'matching phase' if both are at their maximally dorsal positions simultaneously. If one is maximally dorsal when the other is maximally ventral, phasing is called 'alternating'. Duration is the time elapsing as the leg or palp makes a complete cycle, and amplitude is the distance between these positions. The first major segment distal to the point of articulation is referred to in specifying the site of movement: femoral movement, coxa-trochanter joint; tibial, femur-patella; metatarsal, tibia-metatarsus.

For ease of expression, the terms 'up', 'down', forward', 'backward', and 'to the side' are used sometimes for 'dorsally', 'ventrally', 'anteriorly', 'posteriorly', and 'laterally', respectively. The spider's legs are specified as pairs I-IV (anterior to posterior). Expressions such as 'usually' or 'generally', 'sometimes' or 'occasionally', and 'infrequently' or 'rarely' are used to indicate frequencies of occurrence of 80% or more, 20-80%, and 20% or less, respectively. Video tapes of observations were analyzed frame-by-frame. All statistical tests are from Sokal & Rohlf (1981).

Testing with prey

Scytodes was tested with a variety of spiders and insects in the laboratory (TABLE I). Insects were adults and larvae, and spiders were adults and juveniles. All tests were conducted by introducing the prey into a cage containing a *Scytodes* in its web. 'Very small' prey was 0.1-0.25 the size of the *Scytodes* with which it was tested, 'small' prey was about half the size of the *Scytodes*, 'large' prey was equal in size to, or slight larger than, the *Scytodes*, and 'very large' prey was 1.5 - 2.0 times larger than the *Scytodes* (size: estimates of body volume; see Jackson & Hallas, 1986a).

Two types of tests were carried out: Type A and Type B. Each kind of

spider and insect in TABLE I was used in both types of test. During Type A tests, the *Scytodes* and one or more potential prey were kept together and observed for at least 2-4 h. In Type B tests, one potential prey item was offered per *Scytodes* and whether the prey had been captured was determined 24 h later.

Effect of maternal egg attendance on egg survival

In nature, the webs of 50 brooding *Scytodes* females were marked. Half were assigned at random to Group 1 and half to Group 2. Females in Group 1 ('unattended egg sacs') were separated from their egg sacs and removed from the webs (leaving the egg sacs behind in the web), whereas females in Group 2 (controls: 'attended egg sacs') were left in their webs with the egg sacs.

Hatched eggs can normally be seen in *Scytodes*' egg sacs within 4 - 10 days of oviposition. Each marked web was checked daily for 10 successive days or until the first day on which eggs were missing. Any unhatched egg sacs still present after 10 days were collected and dissected.

In the laboratory, 65 adult females were set up with males. After mating, the males were removed and the females maintained until they laid eggs. Most individuals made a single egg sac, and none made more than two. Using 88 egg sacs, two treatment groups were set up, with egg sacs assigned at random to one or the other: 1) attended egg sacs (females left with their egg sacs; N = 52); 2) unattended egg sacs (females separated from egg sacs one week after oviposition and egg sacs kept isolated in the webs; N = 36). Egg sacs were checked every day until juveniles emerged or 10 days elapsed. After 10 days, any remaining egg sacs from which juveniles had not emerged were dissected.

TABLE I

Spiders and insects used in tests with Scytodes in the laboratory

Order	Family	Species	Description	Size*
Araneae	Salticidae	*Euophrys parvula* Bryant[1]	Cursorial jumping spider	S, L
		Jacksonoides queenslandica Wanless[2]	Cursorial jumping spider	VS, S, L
		Marpissa marina Goyen[1]	Cursorial jumping spider	S, L
		Myrmarachne sp.[3]	Ant-like jumping spider	S, L
		Trite auricoma (Urquhart)[1]	Cursorial jumping spider	VS, S, L
		Trite planiceps Simon[1]	Cursorial jumping spider	S, L, VL
Araneae	Lycosidae	*Lycosa* sp.[1]	Cursorial wolf spider	S, L
Mantodea	Mantidae	*Orthodera ministralis* (Fabricius)[1]	Mantis	VL
Blattodea	Blattidae	*Periplaneta americana* (Linnaeus)[4]	Cockroach	VS, S, L, VL
Diptera	Drosophilidae	*Drosophila immigrans* (Sturtevant)[4]	Fruit fly	VS
		Drosophila melanogaster (Meigen)[4]	Fruit fly	VS
	Muscidae	*Musca domestica* (Linnaeus)[4]	House fly	S
	Tipulidae	*Macromastix zeylandia* Alexander[1]	Crane fly	L
	Trichoceridae	*Trichocera annulata* (Meigen)[1]	Crane fly	L
Coleoptera	Coccinellidae	*Coccinella leonina* Linnaeus[1]	Labydird beetle	S

TABLE 1 continues

Order	Family	Species	Description	Size*
Coleoptera	Tenebrionidae	*Tenebrio molitor* Linnaeus[4]	Yellow mealworm	L
Lepidoptera	Noctuidae	*Melancha* sp.[1]	Moth	L
	Tortricidae	*Ctenopseustis* sp.[1]	Moth	L
Hymenoptera	Vespidae	*Vespa germanica* (Fabricius)[1]	Wasp	VL
	Apidae	*Apis mellifera* (Linnaeus)[1]	Bee	VL
	Formicidae	*Chelaner antarctica* (White)[1]	Ant	S
		Huberia striata (Smith)[1]	Ant	S
		Prolasius adveria (Smith)[1]	Ant	S

* Size of spiders and insects used in laboratory tests, where VS, S, L, VL refer to prey that were very small, small, large, or very large relative to the *Scytodes* (see text)
[1] Collected in new Zealand
[2] Collected in Queensland, Australia
[3] Collected in the Philippines
[4] Laboratory culture

Results

Elements of predatory behaviour

The following key behaviours and postures, listed alphabetically with index numbers, will be described: attach silk (11), chase (5), cut thread (9), extended-legs posture (1), feed (12), opened chelicerae and fangs (6), pull (4), retracted-legs posture (2), spit (7), stab (10), tap (3), and wrap (9).

1. *Extended-legs posture*

This posture (legs extended out widely to the side) was generally adopted by *Scytodes* during routine walking. Also, if *Scytodes* was in the retracted-legs posture when prey contacted web lines, *Scytodes* usually switched to the extended-legs posture.

2. *Retracted-legs posture*

The retracted-legs posture was adopted by *Scytodes* at rest. Also, this posture was adopted when an active *Scytodes* was mildly disturbed by a simulation of a predator (a tactile or air-movement stimulus: see Jackson *et al.*, 1990). Legs were held at the sides of the body (laterigrade). Femora of all legs and all segments of leg IV were directed posteriorly, the more distal segments of leg II and III were directed laterally and the more distal segments of leg I were directed anteriorly. The spider's entire body was held close to the substratum so that the spider appeared dorsoventrally compressed. When a *Scytodes* in the extended-legs posture was strongly disturbed by a predator or simulation of a predator, it often switched to the retracted-legs posture.

3. *Tap*

To tap, *Scytodes* adopted a third posture distinctly different from the extended-legs and the retracted-legs posture: legs I and II were held extended almost straight out in front of the body. *Scytodes* tapped by repeatedly flexing then extending by 30° or less the tibia-metatarsus and metatarsus-tarsus joints

of one or more of its legs I & II. Contact was made with the prey, web or substrate on the down stroke. *Scytodes* sometimes tapped 2-5 times in succession using only one leg, but contralateral legs usually moved together in alternating phase (0.5-3/s; 5-20 mm; bouts usually lasting 2-8 s, but sometimes as long as *c.* 30 s). When tapping began, *Scytodes* repeatedly moved legs I slowly from up to down at high amplitude (*c.* 3-10 mm; *c.* 2/s; bouts *c.* 2 s; femoral movement primary). If the legs touched the prey and the prey was active, *Scytodes* switched to moving legs I and II up and down rapidly, but at low amplitude (*c.* 1 mm; *c.* 6/s; bouts *c.* 2 s). Usually, *Scytodes* used legs III and IV to hold its whole body raised while tapping with its forelegs.

4. *Pull*

To pull on the prey, *Scytodes* extended its two legs I while simultaneously raising its body slightly and moving slowly forward to place tarsi I on the prey. Next, legs I flexed to draw the prey in. While drawing the prey in, *Scytodes* lowered its body and retracted its legs I forcefully.

5. *Chase*

Chasing was rapid forward locomotion in which *Scytodes*' speed varied to match that of the prey. It was especially running-away prey that was chased, and usually the chase ended with a final spit (see below) preceded by a pause.

6. *Opened chelicerae and fangs*

Opened chelicerae were held with basal segments spread apart and usually with fangs extended anteriorly. The two extended fangs angled apart from each other by *c.* 90°. Basal segments varied from only slightly spread apart to angled at *c.* 90° to each other.

7. *Spit*

Before spitting, *Scytodes* elevated its body slightly by extending its legs I & II. It spat by opening the chelicerae and fangs and forcefully ejecting a gummy secretion in the direction of prey. The gummy secretion came from the fangs.

Although *Scytodes* occasionally extended, and spat with, only one fang, usually both fangs were extended and apparently used. Spitting was accompanied by a convulsive shudder plus a slight posterior readjustment of the body's position. If the prey struggled hard, *Scytodes* made multiple spits (2-8 spits per bout) and often there were repeated bouts of spitting before the prey was subdued. Each single expulsion of the gummy secretion was accomplished in less than 1/25 s. A net of threads, similar in appearance to the silk from the spider's spinnerets, was left on the prey after spitting attacks.

8. *Cut thread*

To cut a thread, both palps were extended, accompanied by a slight lateral oscillation (*c.* 2 mm), and contacted a thread of dried spit or silk held by the tarsus of a legs I. A single palp pulled the thread upward to place it between the two chelicerae which then held the silk while the palp moved back downward and the thread was severed.

9. *Wrap*

While wrapping, *Scytodes* stood with its body raised 5-10 mm above the substrate and with two legs I extended anteriorly, angling away from each other by *c.* 45°. The two legs II extended rigidly to the side almost perpendicular to the *Scytodes*' longitudinal axis: the two femora were almost parallel to the substrate; the femur-patella joints of these legs were flexed down at *c.* 120° whereas tibia-metatarsus joints were flexed only slightly (*c.* 10°). The prey was held under *Scytodes*' body and between the two arched legs III.

Silk was applied with legs IV. As legs IV moved, their tarsi were drawn across the spinnerets, starting near the metatarsus-tarsus joint, and a thread was caught by the claws. Next, the femur-patella and tibia-metatarsus joints were extended so that the tarsus was brought toward the prey or substrate, then *Scytodes* twisted its tarsus upwards to touch the prey and disengaged the thread before moving the tarsus back to the spinnerets.

Legs IV moved in alternating phase: when one leg IV was at the spinnerets, the other leg IV was placing silk on the prey. Cycle duration

(spinnerets to prey and back) was *c.* 0.5 s if the prey was more or less quiescent. Wrapping rate tended to be about twice this fast if the prey was struggling strongly; even if the prey was not struggling strongly, the *Scytodes* tended to wrap about twice as fast when it first attacked. Occasionally, *Scytodes* made 2-6 wipes with one leg over the prey before the opposite leg was used. Each wipe was accompanied by a lateral movement of the abdomen (10-45°) toward the leg IV which was pulling silk from the spinnerets.

Scytodes used palps and legs III to rotate prey between wrapping bouts: legs III moved the prey (alternating phase, primarily metatarsal movement) forward and up and, at the same time, palps drew the upper side of prey's body backward, so that each side of the prey was rotated toward, then away from, *Scytodes*' body. Wrapping normally followed spitting, and, while wrapping, *Scytodes* partially or completely freed the prey from the substrate. If the prey was only partially freed, *Scytodes* often pulled on the prey forcedly with both palps. *Scytodes* punctuated its wrapping by attaching threads on the prey, the substrate, or nearby threads. Once wrapped, prey was enclosed in a flimsy cocoon of silk.

10. *Stab*

Immediately after spitting, while the prey was being cut free from the spit or while wrapping, *Scytodes* sometimes stabbed by rapidly moving its body forward with fangs pointing toward the prey. When stabbing, prey was not seized with the chelicerae. Instead, *Scytodes*' fangs penetrated the prey, then were removed immediately from punctured prey. Having been stabbed, sometimes prey became immediately immobilized. Other times, the prey struggled and ran away. If the prey was large and struggled, *Scytodes* often stabbed 2-8 times in succession before subduing it.

11. *Attach silk*

To attach silk, *Scytodes* flexed its abdomen toward the attachment site (the prey, the web near the prey or a non-web substrate near the prey). When the attachment site was a web line, this line was pulled to the spinnerets with one of the legs IV.

12. *Feed*

Using its palps to hold the prey against the mouth, *Scytodes* fed by inserting and removing its fangs one or more times, then holding the prey stationary while fluid passed into the *Scytodes*' mouth through the hole made in the prey.

Webs

In the field and laboratory, webs of solitary males and juveniles were similar to those of solitary females, except usually somewhat smaller. Shared webs were similar, except that they tended to be somewhat larger than webs of solitary *Scytodes*. The web consisted of non-sticky lines arranged in a three dimensional mesh under a sheet, usually with a tubular nest linked to the sheet via a small funnel-like opening. The nest was usually 2-4 body lengths long and, at its distal end, not much wider than the spider. In the laboratory, the sheet tended to be more or less circular, with the nest at the centre. In nature, webs were usually found on leaves, which could be living and green or dead, dry and brown. Usually the leaf was partially curled over so that its top surface was concave. The web was usually more or less centred on the top of the leaf, with the nest off to one side. The side of the leaf on which the nest was found was usually more curled over than the rest of the leaf so that the nest was more concealed than the rest of the web. The nest was often placed in a more tightly rolled-up edge of the leaf. The silk of the nest ran into the rest of the web to form the funnel. However, in the field, these tube and funnel shapes were not always so clear, and the curled-up part of the leaf was situated so that the nest had only one opening. Most webs in the field tended to be about 10 mm across.

Twenty-six brooding *Scytodes* females set up individually in large cages stayed with their juveniles in their webs when eggs hatched despite space being available for dispersal. In the laboratory, all sex-age classes of *Scytodes* built webs if in a cage alone. However, juveniles often remained in maternal webs instead of building webs of their own.

Colony composition

The number of solitary and colonial webs are given in TABLE II. These should not be regarded as strictly accurate indications of colony composition of the natural population because: 1) colony webs, being larger, probably were easier than solitary to see; 2) the solitary webs of later instar spiderlings were probably easier than those of smaller individuals to see; and 3) it is difficult to know whether the search in microhabitats likely to harbour solitary and colonial individuals was equalized. However, these data at least serve to indicate the variety of groupings observed, and give some idea of how common each was.

It is interesting that: mature males shared webs with mature females that were both with and without eggs; adult females either died or left webs containing juveniles; webs never contained more than one adult female; adults (males & females) and juveniles of *Scytodes* were found either one per web or in multi-spider groups in a single web, the most common groups being adult females sharing webs with groups of juveniles. If not alone, adult males were most often in webs with adult females. Groups of spiderlings were sometimes found in webs with no female present, although this was uncommon.

Some other trends were evident: 1) males sometimes cohabited with mature females prior to oviposition, but then dispersed or died; 2) since adult females were never seen to share webs, when disparate-sized spiderlings were together in colonies, these were probably offspring of a single female; 3) as the offspring matured, colony size decreased, evidently as a consequence of spiderlings either dying or dispersing as they grew older; 4) sometimes webs contained only juveniles, evidently as a consequence of maternal females dying or abandoning their webs; and 5) *Scytodes* juveniles tended to leave their maternal web to build webs of their own during the third or fourth instar.

TABLE II

Inhabitants of 170 different webs of Scytodes in the field

Inhabitants	No. of observations
Mature female alone	15
Mature male alone	4
Mature female alone with eggs	20
Mature male and mature female	11
Mature male and one later instar juvenile	3
Mature male and group of later instar spiderlings only	2
Mature male and mature female with eggs	2
Mature female and first instar spiderlings only[1]	16
Mature female and mixture of first and later instar spiderlings	27
Mature female and later instar spiderlings only	25
Group of first instar spiderlings only[2]	1
Group consisting of first and later spiderlings but no adult[2]	1
Group of later instar spiderlings only[2]	22
Solitary later instar spiderling	21

[1] First instar is the first stadium and the stage in which the spiderlings disperse from the vicinity of the egg sac.
[2] The size of the web and the strength of the lines strongly suggested that the web the spiderlings inhabited was built by a mature female.

Prey

In nature, there were 112 records of *Scytodes* feeding, with insects accounting for only 14% of the prey records, spiders accounting for the remaining 86% (TABLE III). Salticid spiders were, by far, the most common (71%) prey. Both non-salticid cursorial (6%) and web-building spiders (9%) were among the prey records and one web-invading spider, a mimetid, was among the prey.

Among the insects, dipterans (7%) and hemipterans (4%) were the most common. Also, one moth, one lacewing, one cricket and one mantid were among the prey. There were no records of ants, wasps or beetles among prey in the field, but one ant-like salticid was preyed on. In most (96%) instances, *Scytodes* was either in its web when observed feeding; otherwise (4%), it was in the vegetation within 200 mm of its web.

In Type A and B tests, *Scytodes* never ate wasps, beetles, ants or ant-like salticids, but did attack and eat all other types of insects and all of the types of spiders used (TABLE I).

Capture rates

In Type B tests, the capture rates of *Scytodes* females were high against all kinds of prey used. There was no evidence that *Scytodes* females' capture rates against cursorial salticids was greater than against cursorial lycosids. However, capture rates were significantly greater if the prey was a cursorial lycosid or a cursorial salticid rather than a housefly (TABLE IV). Capture rate was greater on larger than on smaller cursorial salticids, but there was no evidence that prey size affected capture rates when prey were insects (TABLE V).

In Type B tests, when prey were cursorial salticids, capture rates were greater for *Scytodes* females than for males. Capture rates were not significantly different for males and females when prey were cursorial lycosids and insects (TABLE IV). *Scytodes* females had higher capture rates than males against larger cursorial salticids, but there was no evidence that the sexes differed when smaller spiders were used as prey. When prey were insects, there was no evidence that prey size affected capture rates of either sex (TABLE V).

TABLE III

Prey records[1] of Scytodes in the field. Unless noted otherwise, Scytodes in its web when observed feeding

Order	Family	Species	Description	Body length (mm)	Sex-age class	No. of records
Araneae	Anyphaenidae	Unknown	Cursorial spider	4	Juvenile	1
Araneae	Araneidae	*Argiope* sp.	Web-building spider	5	Juvenile	1
		Cyclosa sp.	Web-building spider	3	Juvenile	2
		Gasteracantha sp.	Web-building spider	2	Male	1
		Gasteracantha sp.	Web-building spider	5	Female	1
Araneae	Clubionidae	Unknown	Cursorial spider	4	Juvenile	1
	Gnaphosidae	Unknown	Cursorial spider	3	Juvenile	1
		Unknown	Cursorial spider	4	Juvenile	1
	Lycosidae	Unknown	Cursorial spider	4	Juvenile	1
	Mimetidae	Unknown	Web-invading spider	3	Juvenile	1
	Oxyopidae	Unknown	Cursorial spider	4	Juvenile	1
Araneae	Salticidae	*Cosmophasis* sp.	Cursorial spider	2	Juvenile	1
		Cosmophasis sp.	Cursorial spider	3	Juvenile	3
		Cosmophasis sp.	Cursorial spider	4	Juvenile	1
		Cosmophasis sp.	Cursorial spider	4	Male	1[2]
		Cosmophasis sp.	Cursorial spider	5	Female	2
		Cosmophasis sp.	Cursorial spider	7	Female	1

TABLE III continues

Order	Family	Specis	Description	Body length (mm)	Sex-age class	No. of records
Araneae	Salticidae	*Epeus* sp.	Cursorial spider	3	Juvenile	1
		Epeus sp.	Cursorial spider	4	Juvenile	1
		Epeus sp.	Cursorial spider	5	Juvenile	1
		Epeus sp.	Cursorial spider	8	Male	2
		Epeus sp.	Cursorial spider	8	Female	1[2]
		Harmochirus brachiatus (Thorell)	Cursorial spider	3	Male	1
		Hasarius adonsoni (Audouin)	Cursorial spider	4	Juvenile	1
		Ligurra sp.	Cursorial spider	5	Female	4
		Mantissatta longicauda Cutler & Wanless	Cursorial spider	3	Juvenile	2
		Mantissatta longicauda	Cursorial spider	5	Juvenile	1
		Menemerus bivittatus (Dufour)	Cursorial spider	4	Juvenile	1
		Plexippus sp.	Cursorial spider	4	Juvenile	1
		Myrmarachne sp.	Cursorial spider	5	Female	1
		Simaetha sp.	Cursorial spider	3	Juvenile	1
		Telamonia masinloc Barrion & Litsinger	Cursorial spider	4	Juvenile	1
		Telamonia masinloc	Cursorial spider	6	Male	1
		Telamonia sp.	Cursorial spider	4	Juvenile	2
		Telamonia sp.	Cursorial spider	6	Juvenile	1
		Telamonia sp.	Cursorial spider	7	Juvenile	1
		Unknown	Cursorial spider	2	Juvenile	2

TABLE III continues

Order	Family	Species	Description	Body length (mm)	Sex-age class	No. of records
Araneae	Salticidae	Unknown	Cursorial spider	3	Juvenile	4
		Unknown	Cursorial spider	3	Male	1
		Unknown	Cursorial spider	4	Juvenile	5[3]
		Unknown	Cursorial spider	4	Male	4
		Unknown	Cursorial spider	4	Female	4
		Unknown	Cursorial spider	5	Juvenile	3[3]
		Unknown	Cursorial spider	5	Male	2
		Unknown	Cursorial spider	5	Female	4
		Unknown	Cursorial spider	6	Juvenile	3
		Unknown	Cursorial spider	6	Male	2
		Unknown	Cursorial spider	6	Female	3[3]
		Unknown	Cursorial spider	7	Juvenile	1[2]
		Unknown	Cursorial spider	7	Female	3
		Unknown	Cursorial spider	8	Female	1
		Unknown	Cursorial spider	9	Female	1
		Unknown	Cursorial spider	9	Female	1
		Unknown	Cursorial spider	11	Female	1
Araneae	Tetragnathidae	*Tetragnatha* sp.	Web-building spider	6	Juvenile	1
Araneae	Theridiidae	*Argyrodes* (*Rhomphaea*) sp.	Web-invading spider	4	Female	2
		Argyrodes sp.	Web-invading spider	2	Female	1

TABLE III continues

Order	Family	Species	Description	Body length (mm)	Sex-age class	No. of records
Araneae	Thomisidae	Unknown	Cursorial spider	3	Juvenile	1
Diptera	Drosophilidae	Unknown	Fly	3	Adult	1
	Ephydridae	*Notiphila* sp.	Fly	3	Adult	1
	Dolichopodidae	Unknown	Fly	2	Adult	1
	Dolichopodidae	Unknown	Fly	3	Adult	1
	Dolichopodidae	Unknown	Fly	4	Adult	1
	Micropezidae	*Mimegralla* sp.	Fly	10	Adult	2
	Tephritidae	*Spathulina acroleuca* Schirer	Fly	6	Adult	1
Hemiptera	Delphacidae	*Niloparvata lugani* (Stal)	Brown plant hopper	3	Adult	1
	Delphacidae	*Cofana* sp.		7	Adult	2
	Derbiidae	*Protuista cf. moesta* (Westwood)		5	Adult	1
Lepidoptera	Pyralidae	*Marasima patmalis* Bradley	Moth	8	Adults	1
Neuroptera	Chrysopidae	*Chrysopa* sp.	Lacewing	6	Adult	1
Orthoptera	Gryllidae	Unknown	Cricket	5	Juvenile	1
	Mantidae	Unknown	Mantid	5	Juvenile	1

[1] *Scytodes* in act of feeding in each instance
[2] *Scytodes* in vegetation when observed feeding on this salticid
[3] *Scytodes* in vegetation when observed feeding on one of these salticids

TABLE IV

Results of from Type B tests (see text) using different taxonomic categories of prey. Each individual Scytodes tested, in random order, with each of three types of prey. Tests of independence: males and females compared. Tests of independence also used to compare rate with different types of prey: housefly compared with lycosid, housefly compared with salticid and salticid compared with lycosid. All prey: small. Salticid, lycosid and housefly: introduced to cage containing Scytodes in its web.

		Capture rate (%)		
Prey	N	Female	Male	Comparison
Housefly	59	70	65	NS
Lycosid	21	93	83	NS
Salticid	156	96	75	$P < 0.0001$
Housefly and lycosid compared		$P < 0.05$	$P < 0.05$	
Housefly and salticid compared		$P < 0.0001$	NS	
Lycosid and salticid compared		NS	NS	

TABLE V

Results from Type B tests (see text) using three sizes of salticids and insects as prey. Scytodes males and females compared (tests of independence). Capture rates for very small and large prey compared (tests of independence) separately for males and females. Sample size for each type of test indicated in parentheses

	Prey	Female	Male	Tests of independence
Salticid	Very small	35% (129)	47% (81)	NS
	Small	97% (88)	82% (56)	NS
	Large	93% (72)	54% (63)	$P < 0.0001$
	Very small & large compared	$P < 0.0001$	NS	
Insect	Very small	63% (103)	64% (53)	NS
	Small	70% (108)	73% (45)	NS
	Large	71% (89)	63% (38)	NS
	Very small & large compared	NS	NS	

Predatory sequences

There were two general categories of predatory behaviour: 1) predation in a web; 2) cursorial predation away from webs.

Predation in a web

Scytodes spent most of its time inactive in the retracted-legs posture, either out in the web or, especially, in its nest. However, when potential prey contacted the lines of the web, *Scytodes* usually responded immediately by assuming the extended-legs posture and usually by also fastening a dragline to the web. If the prey was to the side or behind *Scytodes*, then *Scytodes* oriented toward it. If *Scytodes* was in its nest, it left the nest and walked, usually slowly, to the prey while tapping with legs I and II. After touching the prey, *Scytodes* often spat, although *Scytodes* occasionally pulled on the prey before spitting. If the prey struggled strongly, *Scytodes* sometimes spat on it, but more often *Scytodes* moved away, only to return and spit later. Sometimes *Scytodes* spat from as far as 60 mm away prior to contact with the prey. After a successful spitting attack, a net of gum threads covered the prey. The amount of fluid ejected per spit varied with prey size: small prey, tended to receive less fluid per spit; large prey, more fluid per spit.

After spitting, *Scytodes* usually stepped quickly to the prey. However, when prey, especially large prey, struggled vigorously, *Scytodes* usually spat repeatedly before reaching the prey. As the spit dried on the immobilized prey, *Scytodes* often moved toward and stabbed the prey quickly, usually on an appendage. Sometimes stabs were repeated 2-5 times if the prey continued struggling.

After the prey was immobilized, *Scytodes* started to free the prey from the net of gum threads made by spitting. If the prey was not securely fastened, *Scytodes* simply held on with its chelicerae while pushing down on the substratum with all legs and simultaneously lifting up its cephalothorax, thereby pulling the prey free from the net of spit. If the prey had become securely fastened by a spit net, *Scytodes* usually cut through the securing threads. Once prey was either completely freed or had only one side attached to the substrate, *Scytodes* began to wrap up the prey. Finally *Scytodes* held the trussed-up prey

in its chelicerae and began to feed. *Scytodes* fed on prey either at the capture site or carried the prey to its nest, then fed. Feeding usually lasted *c.* 60 min (range 30 -150 min).

Prey capture away from webs

On five occasions, *Scytodes* in nature was seen away from webs feeding on salticids (TABLE II), and numerous away-from the web predatory sequences were seen in the laboratory.

Predatory sequences that began with *Scytodes* in its web in the laboratory were sometimes completed outside. For example, a capture sequence might begin when prey contacted the web, but when the prey left the web, *Scytodes* sometimes chased after it, left the web completely, attacked by spitting and captured the prey. Web departure was about equally often while *Scytodes* was turning or walking toward the prey prior to contacting it, while tapping the prey prior to spitting on it or after having spat once or twice but having failed to immobilize the prey.

Also, *Scytodes* sometimes left the web completely to go on hunting forays in the vegetation. Away from webs, *Scytodes* appeared to detect prey movement through leaf or stem surfaces alone, with no involvement of web lines at all. Generally, these sequences began with *Scytodes* actively walking about on the vegetation and tapping slowly. If *Scytodes* touched a prey, tapping became rapid, then *Scytodes* pulled on the prey and spat. If the prey ran away, *Scytodes* chased after it, paused, then spat at the prey.

Other times, capture sequences began before *Scytodes* tapped the prey. Apparently having detected, through the vegetation, vibration caused by movement of active prey, *Scytodes* became quiescent for several seconds, then walked slowly in the direction of the prey. *Scytodes* usually drew back a few millimetres, then spat on the prey that approached *Scytodes* slowly from in front and got to within about 10 mm. If the prey was moving rapidly and passed the *Scytodes* from in front, *Scytodes* often spat suddenly. After spitting on and wrapping the prey, *Scytodes* occasionally carried the prey back to the web before completing feeding, but it usually fed on it at the capture site.

If, while hunting away from its webs, a salticid was walking in its typical stop-and-go gait on the leaf shared by a *Scytodes*, the *Scytodes* usually turned toward the salticid, then approached it slowly. Once close, if the salticid turned to face it, *Scytodes* usually stopped walking; If the salticid next ran away, *Scytodes* chased after the salticid and, when close behind the salticid, paused briefly then attacked by spitting.

Small salticids were usually immobilized quickly by *Scytodes*' spit. However, against large, struggling salticids, *Scytodes* often spat 2-4 times in succession and made multiple stabs before the prey was immobilized.

Prey rejection

When tested in the laboratory, *Scytodes* usually failed to approach bees, wasps, and beetles, and moved away when they came close. When *Scytodes* and these insects did occasionally make contact, *Scytodes* moved away quickly and did not return. If one of these insects moved toward or passed close to a *Scytodes*, *Scytodes* sometimes suddenly spat, but never approached. If the spat-on bee, wasp, or beetle ran away, *Scytodes* never chased after it.

Scytodes was never observed to approach or spit at an ant. Even when an ant moved toward *Scytodes*, *Scytodes* moved away and did not spit. When tested with ant-like salticids (*i.e.*, *Myrmarachne* sp.), *Scytodes*' reactions were usually similar to how it reacted ants. However, in two instances in which ant-like salticids walked rapidly toward *Scytodes*, *Scytodes* suddenly spat, then moved away and never returned. The gummed down *Myrmarachne* eventually freed itself.

Observations of juveniles

As with most spider species, spiderlings of *Scytodes* emerged from the egg sac are in the first instar (for terminology, see Hallas, 1988). Females carried egg sacs in their chelicerae until the spiderlings emerged. Spiderlings tended to stay in the nest for first 15 days after emergence. However, when artificially separated them from their mother's web, these spiderlings built small webs of their own and were successful at prey capture by spitting.

About 15 days after emergence from the egg sac, the spiderlings moulted into the second instar, became more active, moved out from the nest and spread about in their mother's web. Occasionally, a few spiderlings left the maternal web voluntarily in the second instar. These, and other second-instar spiderlings artificially separated from the maternal web, readily spun their own webs. Second-instar spiderlings, whether in their mother's web, in their own webs, or away from webs, sometimes attacked prey by spitting and, when they did so, their behaviour during predatory sequences was, in basic respects, similar to that of adults. However, second-instar spiderlings generally were, compared to larger juveniles, reluctant to spit.

Most spiderlings began to leave their mother's web voluntarily just after the second moult (*i.e.*, in the third instar), although a few remained until the fourth instar. Third and all subsequent instar spiderlings could be readily induced to spit and carry out typical capture sequences.

Maternal behaviour

In nature, females were often found in webs, not only with egg sacs containing unhatched eggs, but also with juveniles of various sizes, although spiderlings in the first and second instar were the most common (for definitions, see Li, 1995). In the laboratory, *Scytodes* females that had egg sacs or juveniles recently emerged from the eggsac always stayed in their webs. Juveniles generally stayed in the maternal nest until after the second moult, then moved out into mesh and sheet while in their second instar. They tended to stay in the mesh and sheet of the maternal web up until the third moult, then left and built their own webs during the third instar.

Females sharing webs with juveniles readily attacked prey in the web by spitting, but they did not spit at the juveniles walking in the web. Juveniles captured small prey that landed on the sheet, but did not spit at each other or their mother. Juveniles also scavenged on prey or remains of prey captured by the adult female and left in the web. Cannibalism was never seen.

Upon introducing prey on to a web shared by an adult female and a group of juveniles, the female usually walked out of her nest, then approached, spat at

and wrapped the prey. Next she took the prey to the sheet and mesh where juveniles waited. Most individual juveniles walked toward and fed on the wrapped prey together. Sometimes, especially if there was no adult in the web to do the wrapping, a group of juveniles wrapped the prey together.

In the field and the laboratory (TABLE VI), the survival of attended egg sacs was significantly higher than that of unattended egg sacs (for field data, $X^2 = 23.53$, $P < 0.001$; for laboratory data, $X^2 = 51.34$, $P < 0.001$). In the field, all of the 25 attended egg sacs, but only 9 (36%) of the 25 unattended egg sacs survived and hatched. Eleven (69%) of the 16 unhatched egg sacs in the field simply disappeared, presumably having been taken by predators; four were seen being attacked by ants; two were infested with mites and one was desiccated.

TABLE VI

Effect of Scytodes female's presence on egg-sac survival (see text)

Treatment	N	Hatched	Ants	Mites	Mould	Dry	Missing
Attended in field	25	25 (100%)	0	0	—	0	0
Unattended in field	25	9 (36%)	4 (25%)	2 (13%)	—	1 (6%)	9 (56%)
Attended in laboratory	52	48 (92%)	—	2 (50%)	2 (50%)	0 (0%)	—
Unattended in laboratory	36	6 (17%)	—	11 (37%)	12 (40%)	7 (23%)	—

N: total number of egg sacs. Hatched: No. of egg sacs that hatched (percentage of N). Mould: No. of unhatched egg sacs with mould on eggs (percentage of unhatched egg sacs). Mites: No. of unhatched egg sacs with mites on eggs (percentage of unhatched egg sacs). Dry: No. of unhatched egg sacs containing only desiccated eggs (percentage of unhatched egg sacs). Missing: No. of egg sacs that vanished from web before seen to have hatched (percentage of unhatched egg sacs)

In the laboratory (TABLE VI), 48 of the 52 attended egg sacs (92%), but only 6 of the 36 (20%) unattended egg sacs survived and hatched. Of the 34 egg sacs that failed to hatch, 27 (79%) were infested with mould or mites and seven (21%) were desiccated, but the prevalence of these factors varied with treatment: 64% of the unattended egg sacs were infested with mould or mites *vs* 8% of the attended egg sacs ($X^2 = 34.47$; $P < 0.001$); 19% of the unattended egg sacs were desiccated *vs* none of the attended egg sacs ($X^2 = 8.49$; $P < 0.005$).

Discussion

Predation on salticids

Although *Scytodes* fed on a wide variety of insects and spiders in nature, salticid spiders were the dominant prey. Also, in the laboratory, *Scytodes* caught a wide variety of prey types, but salticids were caught especially often. Routine predation on salticids is noteworthy, as this has otherwise been reported in the feeding repertoire of only one other spider, *Portia fimbriata* from Queensland (Jackson & Blest, 1982a; Jackson & Hallas, 1986a).

Salticids, being abundant in *Scytodes*' microhabitat (leaf surfaces), are probably encountered commonly, and frequent encounters must be one factor explaining why *Scytodes* includes so many salticids in its diet. Also, the typical stop-and-go gait of many salticids appears to be especially effective at triggering *Scytodes*' attack. Perhaps *Scytodes* has evolved particular sensitivity to the vibrations made by typical salticid walking gaits. Also, it may be that *Scytodes* is especially good at catching salticids because of its spitting attacks. By spitting quickly, *Scytodes* appears to have a weapon with which to subdue the salticid from a distance (5-20 mm) before the salticid detects the presence of a potential predator.

Often *Scytodes* caught salticids using its web. Some spiders build sticky webs, and this kind of web can ensnare prey for long periods (Shear, 1986; Hallas & Jackson, 1986). However, the Los Banos *Scytodes*, other *Scytodes* species (Kullmann & Stern, 1981; Nentwig, 1985) and many other spiders build

webs that are not sticky and appear to function not so much as snares but more as information-gathering devices which extend the spider's tactile sensory range (see Witt, 1975; Masters *et al.*, 1986). For the Los Banos *Scytodes*, the web may be especially important for gathering information about salticids hunting on the leaf.

In broad respects, prey capture by the Los Banos *Scytodes* when on its own web was similar to that of *Scytodes* sp. from North America (Gilbert & Rayor, 1985). However, the present study has provided more detail about predation, included consideration of prey capture away from webs and revealed a complex predatory strategy.

The Los Banos *Scytodes* builds a web, but catches prey both in and away from its web. This species also varied its behaviour in relation to prey size: it tended to spit at small prey only once; but spat multiple times at large prey. Not only the number of spits but also the amount of fluid ejected per spit appeared to vary with prey size. In addition to *Scytodes*' apparent ability to fine-tune spitting behaviour to prey size, there may also be behavioural flexibility in relation to use of stabbing and wrapping behaviour. Perhaps frequent predation on a potentially dangerous prey - salticid spiders - requires especially complex predatory abilities (see Jackson, 1992a).

Rejected prey

In the field, *Scytodes* was never seen eating ants, bees, beetles, or wasps, and *Scytodes* also avoided these prey in the laboratory. Ants have strong mandibles, poisonous stings and formic acid (Eisner, 1970; Blum, 1981; Hölldobler & Wilson, 1990). Bees and wasps bite and sting. Also, being social insects, ants, bees and wasps tend to be present in large numbers and can mount communal attacks on predators and prey. Beetles have hard exoskeleton and many species have chemical defences (Edmunds, 1974). All of these factors tend to present formidable challenges to most spiders (Nentwig, 1986).

It is interesting that *Myrmarachne*, a genus of jumping spiders which resemble ants in body form and locomotory behaviour (Wanless, 1978), tended not to trigger attacks by *Scytodes*. In laboratory tests, none were attacked. In the

field, although various species of *Myrmarachne* are numerous on the leaves in *Scytodes*' habitat, only one instance was observed of *Scytodes* feeding on a *Myrmarachne*. This observation implies that *Myrmarachne* is, for *Scytodes*, edible, and also raises questions about why *Myrmarachne* is rarely attacked.

Many potential predators with good eyesight that would eat salticids, but are adverse to eating ants, probably mistake *Myrmarachne* for ants and, therefore, fail to attack these salticids (Englehardt, 1970; Jackson, 1986b; Cutler, 1992; Jackson & Willey, 1994). Against these predators, *Myrmarachne*'s resemblance to ants probably functions as Batesian mimicry (Edmunds, 1974).

Scytodes has simple eyes and poor eyesight. However, *Myrmarachne*'s walking gait resembles that of an ant, and contrasts with the stop-and-go gait of typical salticids, suggesting that *Scytodes* may perceive web-vibration signals from ants and *Myrmarachne* as similar. This appears to be the first evidence to suggest that *Myrmarachne* is a Batesian mimic of ants in a modality other than vision.

Maternal behaviour and sociality

A routine component of the Los Banos *Scytodes*' web is a nest which is tubular in shape and usually more densely woven than the surrounding sheet and mesh. *Scytodes* takes refuge in the nest when not active, small juveniles spend most of their time within, and the nest probably affords protection against predators both by hiding the spiders inside from detection by predators with good eyesight and by presenting a mechanical barrier to small web-invading predators.

However, the nest is not the full extent of *Scytodes*' maternal care. Maternal care in animals can be defined broadly to include the preparation of nests and burrows, the production of large, heavily-yolked eggs, the care of eggs before, and young after, hatching, and the care of offspring after nutritional independence (Clutton-Brock, 1991). In many spiders, maternal care appears to be limited to the making and placement of an egg sac, which is then abandoned shortly afterwards (Gertsch, 1949; Peck & Whitcomb, 1970; Turnbull, 1973; Christenson & Wenzl, 1980). However, there are also many spiders that carry or otherwise attend eggs sacs (Comstock, 1948; Bristowe, 1958; Horel &

Gundermann, 1992), but the function of egg attendance is unclear for most spiders (see: Fink, 1986; Horel & Gundermann, 1992).

Functions that have been proposed for spider maternal behaviour include defending eggs from attacks of predators (Gertsch, 1949; Bristowe, 1958; Eberhard, 1974; Foelix, 1982; Horel & Gundermann, 1992) and parasites (Lubin, 1974; Horel & Gundermann, 1992), regulating water balance of eggs (Bonnet, 1930, 1946; Bradoo, 1973), regulating temperature of eggs (Norgaard, 1951, 1956; Vlijim *et al.*, 1963; Shear, 1970; Bradoo, 1973; Humphreys, 1974), providing food for young (Norgaard, 1956; Bristowe, 1958; Kaston, 1965; Shear, 1970; Buskirk, 1981), alerting young to the presence of danger or food (Norgaard, 1956), and opening the egg sac to enable the spiderlings to emerge (Gertsch, 1949; Engelhardt, 1964; Whitcomb & Eason, 1967; Randall, 1977; Fujii, 1978; Tahiri *et al.*, 1989).

In the present study, unattended egg sacs often failed to hatch both in the field and in the laboratory. Many unhatched eggs were desiccated, suggesting that *Scytodes* females may protect egg sacs against water loss. How they might achieve this is unclear.

Egg attendance may function in many species to protect against predators (Fink, 1986, 1987; Willey & Adler, 1989; Ruttan, 1991; Horel & Gundermann, 1992). For example, females of *Peucetia viridans* (Oxyopidae), a large vagrant spider, attend their eggs and thereby reduce predation by ants (Fink, 1986; Willey & Adler, 1989). Ants, which were common on the leaves occupied by the Los Banos *Scytodes* in the field, appear also to be important predators on the eggs of the Los Banos *Scytodes*. Four attacks by ants on unattended eggs were seen, and unattended egg sacs that disappeared in the field study may also have been taken by ants.

Unattended eggs of *Scytodes* sp. were also attacked by mould and mites in the laboratory, as has been shown in laboratory studies of *Peucetia viridans* (Willey & Adler, 1989) and *Coelotes terrestris* (Horel & Gundermann, 1992). However, whether the mould and mites caused the death of the eggs or whether they infested eggs that were already killed by other causes is unclear. Protection against parasites has also been suggested as a function of egg attendance

(Kessler & Fokkinga, 1973; Lubin, 1974; Horel & Gundermann, 1992), but no evidence related to this is available in *Scytodes*.

The Los Banos *Scytodes* also provisioned young with food after hatching. Females attacked and wrapped up prey, especially salticids, then took the prey back to the vicinity of the young and left it for the juveniles to feed on.

Using the terminology prevalent in the literature on social insects and spiders (Wilson, 1971; Aviles, in press), *Scytodes* sp. appears to be a subsocial species. Pronounced social behaviour is known also in *Scytodes intricata* in Panama (Eberhard, 1986), and *Scytodes fusca* in Queensland, Australia (Bowden & Jackson, 1988). All three species, *S. fusca*, *S. intricata* and *Scytodes* sp., tend to live communally. The largest colonies are those of *S. fusca*, a communal and territorial social spider (definition: Jackson, 1979) that builds web complexes on three trunks. Many individuals, including many adults of this species, live together in these complexes, but with adults occupying their separate defended web units (Bowden & Jackson, 1988). Neither *S. intricata* nor the Los Banos *Scytodes* have been seen in web complexes.

In *S. intricata* and the Los Banos *Scytodes*, one adult per web was the rule, except for male-female pairs. Colony members of *S. intricata* and of the Los Banos *Scytodes* appear to be mother and offspring. Yet the body size of the juveniles in groups varied considerably.

In both *S. intricata* and the Los Banos *Scytodes*, group members routinely fed together on the same prey. However, these two species appear to differ: *S. intricata* females, unlike females of the Los Banos *Scytodes*, appear not to provision juveniles with food or share prey with juveniles. Also, intraspecific aggression and even cannibalism were seen in *S. intricata*, but not in the Los Banos *Scytodes*. Evidently, a considerable range of social behaviour has evolved within the genus *Scytodes*.

CHAPTER 7

Predator-prey interactions between web-invading jumping spiders (Araneae: Salticidae) and *Scytodes* sp. indet. (Araneae: Scytodidae) from Los Banos, the Philippines

Abstract: Four species of jumping spiders (Salticidae), with different predatory strategies, were tested in the laboratory with *Scytodes* sp. indet., a web-building spitting spider from the Philippine: *Ligurra* sp. from the Philippines leapt into webs, whereas *Portia fimbriata* from Queensland (Australia), *P. labiata* from Sri Lanka, and *P. labiata* from the Philippines walked slowly into webs and practised aggressive mimicry. These species captured *Scytodes*. *Jacksonoides queenslandica* which is known to be a web-invader never attacked *Scytodes*. *P. fimbriata* and *P. labiata* were more efficient than *Ligurra* sp. at catching *Scytodes*. *P. fimbriata* from Queensland was more consistent at using aggressive mimicry than were *Portia labiata* from Sri Lanka and *P. labiata* from the Philippines, but was less efficient at catching *Scytodes*. *P. labiata* from the Philippines was more inclined to undertake aggressive mimicry-detour-leap sequences (*Scytodes*-specific capture behaviour) than were the Queensland *P. fimbriata* and the Sri Lanka *P. labiata*, and the use of this behaviour appears to have been responsible for greater effectiveness at catching *Scytodes* and avoiding being spat on by *Scytodes*.

Introduction

Scytodidae is a family of predominantly tropical and subtropical spiders, best known for the genus *Scytodes*. There appear to be about a half dozen species in this genus, all of which use an unusual (and, in spiders, apparently unique) predatory and anti-predatory behaviour: they spit a sticky gum from their chelicerae over prey and predators (Monterosso, 1927; Bristowe, 1958; Dabelow, 1958; McAlister, 1960; Gilbert & Rayor, 1983). *Scytodes* sp. indet. from Los Banos, the Philippines, is an especially interesting spitting spider because it preys especially on jumping spiders (Salticidae) (Chapter 6) and is, in turn, especially often the prey of jumping spiders.

In nature, *Scytodes* sp. indet. (hereafter, just '*Scytodes*') lives primarily on large leaves of trees and shrubs, where it builds a skimpy non-sticky web. Salticids are very common in the same habitat, foraging on the same leaves. As is typical of web-building spiders, *Scytodes* has poor eyesight, and it is apparently vibratory signals from salticids moving about on the leaf or, especially, touching the web that elicits spitting attacks by *Scytodes* (Chapter 6).

Species in the salticid genus *Portia* are known as web-invading aggressive mimics that specialize in araneophagy (Jackson, 1992a). In Los Banos, *P. labiata* lives in the same habitat as *Scytodes*, hunts on the same leaves and especially often feeds on *Scytodes* (Jackson, unpubl. data). *Ligurra* sp. is another salticid which, although not an aggressive mimic, has been seen eating *Scytodes* in nature. However, the techniques used by *P. labiata* and *Ligurra* sp. to catch this salticid-eating spider have not been studied previously.

Salticids have complex eyes and acute vision (Land, 1969a, b; Blest *et al.*, 1990), and most species appear to be insectivores that hunt in the open instead of building or invading webs. A minority of species ('web invaders', see Jackson, 1986a), however, routinely walk or leap into alien webs to prey on resident spiders, and a still smaller minority practises aggressive mimicry (Jackson, 1992a).

In their predatory strategies, aggressive-mimic salticids are among the most behaviourally complex invertebrates (Jackson, 1992a; Jackson & Pollard, 1996). Of the aggressive-mimic salticids, species in the genus *Portia* are of particular interest. Five of the fourteen species in this genus (Wanless, 1984) have been studied (Jackson & Hallas, 1986a). *Portia* is also of interest because of interspecific and interpopulation variation in predatory behaviour (Jackson & Hallas, 1986a), apparently a consequence of local adaptation to locally abundant prey (Jackson, 1992b). The Queensland population of *P. fimbriata* is known to be more consistent than other species of *Portia* and other populations of *P. fimbriata* at using aggressive mimicry and more efficient at catching a wide range of web-building spiders (Jackson & Hallas, 1986a). Whether *Portia* has specialized predatory behaviour for catching *Scytodes* is of particular interest: *Portia* and *Scytodes* are, for each other, simultaneously potential prey and potential predators.

Materials and methods

Maintenance, testing procedures, cage design, terminology and conventions for describing behaviour followed other spider studies (Jackson & Hallas, 1986a; Jackson, 1990c; Jackson, 1992c, d, e). Only essential details are given here.

The salticid species used are listed in TABLE I, and more information about the predatory behaviour and habitats of these species can be found in the references. The web-invading salticid spiders used were *Portia fimbriata* (Jackson & Blest, 1982a) and *Jacksonoides queenslandica* (Jackson, 1988) from Queensland, *P. labiata* and *Ligurra* sp. from Los Banos, the Philippines, and *P. labiata* from Sri Lanka (Jackson & Hallas, 1986a). *Ligurra* sp., which is sympatric with *Scytodes*, and *Jacksonoides queenslandica* were chosen as a representative web-invading salticids that do not use aggressive mimicry.

TABLE I

Salticid species used in tests with Scytodes

	Typical body length of adult female (mm)	Collection site
Jacksonoides queenslandica	6	Cairns, Queensland, Australia
Ligurra sp.	6	Los Banos, the Philippines
Portia fimbriata (Q)	8	Cairns, Queensland, Australia
Portia labiata (LB)	8	Los Banos, the Philippines
Portia Labiata (SL)	8	Peradoniya & Kaneliya, Sri Lanka

Queensland *P. fimbriata*, Los Banos *P. labiata* and Sri Lanka *P. labiata* will be referred as *P. fimbriata* (Q), *P. labiata* (LB) and *P. labiata* (SL), respectively (TABLE I), and *Ligurra* sp. will be simply referred as *Ligurra* throughout this chapter.

Tests of salticid-*Scytodes* interactions were staged by introducing a single individual of the salticid into the bottom of each *Scytodes*' cage and observing it for 4 h, or until either spider was killed. Each *Scytodes* tested was an adult female. Salticids were adults or juveniles chosen to be comparable in body size to the body size of the *Scytodes*. *Scytodes* and predators were kept without food for 24-48 h and 5-7 days, respectively, before each test. All tests were carried out in the laboratory in Christchurch. An individual spider (salticid or *Scytodes*) might be used in more than one type of test, but each test of a given type was carried out with a different spider.

By definition, a pursuit occurred when a salticid leapt toward a *Scytodes* into the web from outside, walked slowly across the web toward a *Scytodes*, or performed aggressive mimicry displays. The term 'detour' was defined as indirect routes taken by a salticid to reach prey (Curio, 1976).

Data analysis and presentation

When there were no evident differences between *Portia fimbriata* and *Portia labiata* or between the two different populations of *P. labiata*, data were pooled and referred to simply as '*Portia*'. Generally, only comparisons for which there was a significant difference between data sets will be discussed. Comparisons were made using Chi-square tests of independence.

Results

Salticids tested differed in how often they pursued and captured *Scytodes* and in how often they were spat at and captured by *Scytodes* (TABLE II). *Jacksonoides queenslandica* never pursued, invaded the webs of and captured *Scytodes*. All types of the *Portia* (*P. fimbriata* (Q), *P. labiata* (SL) and *P. labiata* (BL)), however, almost always pursued the *Scytodes*, and they did not differ significantly in pursuit tendency. However, *P. labiata* (LB) had a greater capture efficiency (80%) than *P. fimbriata* (Q)(31%)($P < 0.001$, Chi-square tests of independence) and *P.* labiata (SL)(42%)($P < 0.01$). *Ligurra*, compared with

Portia, was less inclined than all *Portia* to pursue *Scytodes* (pooled data for all *Portia*, $P < 0.001$: TABLE II). When *Ligurra* did pursue *Scytodes*, it was less efficient at catching *Scytodes* than *P. fimbriata* (Q)($P < 0.01$), *P. labiata* (SL)($P < 0.001$), or *P. labiata* (LB)($P < 0.0001$).

TABLE II

Salticid-Scytodes interactions expressed as percentage of tests in which each behaviour occurred

	No. of tests	*Scytodes* Spat (%)	Salticid pursued *Scytodes* (%)	Salticid's capture efficiency* (%)	*Scytodes* captured salticid (%)
Jacksonoides queenslandica	34	90	0	-	90
Ligurra sp.	29	62	45	17	45
Portia fimbriata (Q)	54	38	96	31	19
P. labiata (SL)	38	29	98	42	16
P. labiata (LB)	65	15	98	80	8

* Percentage of pursuits by salticids that ended with salticid capturing *Scytodes*. All other percentages are of No. of tests

Ligurra always attacked *Scytodes* by leaping. *Portia*, however, sometimes combined aggressive mimicry with a final attack by leaping, but also attacked by leaping without first using aggressive mimicry (TABLE IV). Alternatively, *Portia* entered webs and pursued *Scytodes*, with or without moving its legs and palps on the web to make aggressive mimicry signals.

However, vibration behaviour associated with the characteristics (rate, duration, amplitude) of specific individual elements varied among *Portia* (TABLE III). After entering the webs of *Scytodes*, all *Portia* usually remained on *Scytodes*' webs for 1 - 31 min (media: 12 min), then began to vibrate webs with palps (usually) and legs (occasionally). Three types of signalling by use of palp

described before for *Portia* also occurred in interactions between *Portia* and *Scytodes*. 1) *Portia* fluttered by making very rapid oscillations (durations: *c.* 1/25 s-1/10 s; amplitude: *c.* 1 mm) of forward-extended palps against the silk, usually with 3-5 complete oscillations per bout. 2) To strike, palps were raised (durations: *c.* 1/4 s; amplitude: *c.* 2-3 mm) then lowered rapidly (durations: *c.* 1/25 s) and forcefully onto the silk. Generally only one strike occurred at a time, with the two palps moving in phase. 3) *Portia* plucked by forcefully pulling, pushing, or both on the silk one or more times with both palps.

While making aggressive mimicry signals in the webs of *Scytodes*, *P. fimbriata* (Q) was more inclined than *P. labiata* (LB)(7%)($P < 0.01$) and *P. labiata* (SL)(16%)($P < 0.05$) to vibrate webs by fluttering alone (33%). *P. fimbriata* (Q) was also more inclined to vibrate webs by fluttering and striking together (32%) than *P. labiata* (LB)(11%)($P < 0.05$). However, *P. labiata* (LB) was more inclined to vibrate webs by plucking alone (65%) than *P. fimbriata* (Q)(11%)($P < 0.001$) and *P. labiata* (SL)(37%)($P < 0.05$). There was no evidence that how frequently webs were vibrated by striking alone or by fluttering, striking and plucking together differed among the types of *Portia* tested (TABLE III). Over all *P. labiata* (SL) and, especially, *P. labiata* (LB) vibrated *Scytodes*' webs more slowly and gently than *P. fimbriata* (Q). If *Scytodes* responded (*i.e.*, oriented toward *Portia* or went out its nest), *P. labiata* (SL)(37%)($P < 0.05$) and *P. fimbriata* (Q)(85%)($P < 0.001$) were more inclined to continue vibrating webs and also to begin to approach *Scytodes* directly than was *P. labiata* (LB)(12%). *P. labiata* (LB) was more inclined to cease web vibration immediately (88%) than *P. fimbriata* (Q)(15%)($P < 0.001$) and *P. labiata* (SL)(63%)($P < 0.05$)(TABLE III).

P. fimbriata (Q) used aggressive mimicry (95%) more often than *P. labiata* (SL) (70%)($P < 0.01$) and *P. labiata* (LB)(88%)($P < 0.05$), but both *P. labiata* (SL)(64%) and *P. labiata* (LB)(77%) pursued *Scytodes* by leaping (71%, pooled data) more often than *P. fimbriata* (Q)(27%)($P < 0.001$)(TABLE IV). *P. labiata* (SL)(14%) and *P. labiata* (LB)(5%) pursued *Scytodes* by walking into webs (*i.e.*, not leaping or using aggressive mimicry)(9%, pooled data) more often than *P. fimbriata* (Q)(0%)($P < 0.01$)(TALE IV). *P. fimbriata* (Q) used aggressive mimicry and did not leap at all in 65% of the tests, but *P. labiata* (LB) and *P. labiata* (SL)

TABLE III

Occurrence of individual vibration behaviour in tests during which Portia pursued Scytodes using aggressive mimicry. Occurrence of each behaviour element expressed as numbers of tests during which the behavioural element(s) occurred divided by the total number of tests during which Portia performed aggressive mimicry and multiplied by 100

	Portia fimbriata (Q)	*Portia labiata* (SL)	*Portia labiata* (LB)
No. of tests during which aggressive mimicry was performed	40	38	46
Flutter alone	33%	16%	7%
Strike alone	16%	18%	13%
Flutter and strike	32%	21%	11%
Pluck alone	11%	37%	65%
Flutter, strike and pluck	8%	8%	4%
Continued vibrating immediately after *Scytodes responded*	85%	37%	12%
Ceased to vibrate webs immediately after *Scytodes* responded	15%	63%	88%

used aggressive mimicry without leaping at all in only 6% and 11% of the tests, respectively. *P. fimbriata* (Q) also rarely leapt without first using aggressive mimicry (4%)(TABLE IV).

Portia also practised another mode of pursuit - taking a detour. After performing web vibrations, if *Scytodes* responded, *Portia* usually fixated on the *Scytodes*, remained quiet on the web for a variable time (1 - 30 min), then turned *c.* 30-180° (median: 71.5°) away to begin an indirect route. *Portia* usually walked along the edge of the leaf (71%) on which *Scytodes* built the web, sometimes left the leaf to reach the wall of the cage (21%), and occasionally went to the back side (*i.e.*, side opposite the web) of the leaf (8%). Individual *Portia* that made a detour across the leaf (*i.e.*, walked along the edge of leaf or crossed the back of leaf) reached a point on the leaf 10-30 mm above the web but facing away from *Scytodes* 30-195 min (median: 68 min) after turning away to begin detouring. Individual *Portia* that went completely away from leaf and on to the wall of the cage usually reached the top of cage above the leaf, and took a long time (23-234 min; median: 83 min) to reach this point.

Portia was more efficient at catching *Scytodes* when taking a detour than when using other methods of pursuit: 94% for taking detours and use of aggressive mimicry with final attack by leaping *vs* 58% for use of aggressive mimicry and leaping but not taking detour, $P < 0.001$; 67% for taking detour and use of aggressive mimicry but not leaping *vs* 21% for use of aggressive mimicry alone, $P < 0.01$; 88% for all tests with detours *vs* 23% for all tests without detours (*i.e.*, leapt, used aggressive mimicry or both, or walked into web), $P < 0.001$.

P. labiata (SL) and *P. labiata* (LB) were more inclined to pursue the *Scytodes* by taking detours ($P < 0.001$; pooled data) and had a greater capture efficiency ($P < 0.01$, see TABLE II) than *P. fimbriata* (Q). There was no evidence that *P. labiata* (LB) used aggressive mimicry or leapt at *Scytodes* more often than *P. labiata* (SL)(TABLE IV), but *P. labiata* (LB) was more inclined to pursue the *Scytodes* by taking detours (71%) than was *P. labiata* (SL)(35%)($P < 0.01$) and had a greater capture efficiency (80%) than *P. labiata* (SL)(42%)($P < 0.01$, see TABLE II).

TABLE IV

Methods used by Portia to pursue Scytodes

	P. fimbriata (Q)	*P. labiata* (SL)	*P. labiata* (LB)
Total number of tests with pursuits	52	37	63
Portia moved into web but did not use aggressive mimicry or leap (%)	0	14	5
Portia used aggressive mimicry but not leap (%)	65	11	6
Portia leapt but did not use aggressive mimicry (%)	4	16	6
Portia used aggressive mimicry and leapt but did not make detour (%)	17	24	11
Portia used aggressive mimicry and made detour but did not leap (%)	7	11	11
Portia used aggressive mimicry, made detour and leapt (%)	6	24	60
Total: *Portia* leapt (%)	27	64	77
Total: *Portia* used aggressive mimicry (%)	95	70	88
Total: *Portia* made detour (%)	13	35	71

Although *P. labiata* (LB) took detours more frequently than did other *Portia* (TABLE III), this alone does not explain why *P. labiata* (LB) was more efficient than other *Portia* when not taking a detour. Excluding instances in which *Portia* took detours, *P. labiata* (LB) was still more efficient than other *Portia* at catching *Scytodes* when using aggressive mimicry only (75% for *P. labiata* (LB) vs. 16% for all other *Portia*, $P < 0.01$), and *P. labiata* (LB) did not differ significantly in capture efficiency from other *Portia* when not using aggressive mimicry (TABLE III). Probably the population of *P. labiata* from Los Banos practised aggressive mimicry more effectively than the other *Portia*.

Ligurra captured *Scytodes* by leaping. However, when *Portia* did leap, it was more efficient (83%) than *Ligurra* at catching the *Scytodes* (17%)($P < 0.001$).

Sometimes (23%) *Portia* elicited spitting while walking in a web toward a *Scytodes* or performing aggressive mimicry, but rarely (4%) while taking detours to attack the *Scytodes* from behind. *Portia* was less inclined to elicit spitting (27%) than was *Ligurra* (62%)($P < 0.05$) and *J. queenslandica* (90%)($P < 0.001$)(TABLE II). *P. labiata* (LB) was less inclined to elicit spitting (6%) than other *Portia* (*P. fimbriata* (Q)(29%), $P < 0.01$; *P. labiata* (SL)(17%), $P < 0.05$) while performing aggressive mimicry displays.

If spat on, *Portia* was less likely than *Ligurra* ($P < 0.01$) to be killed: 50% of the spat-on *Portia* compared with 72% of the spat-on *Ligurra* were killed. Apparently, *Portia* was less vulnerable because, compared to *Ligurra*, it had little difficulty walking or running on the *Scytodes*' web. Also, *P. labiata* performs wild leap (suddenly jump up once or twice on a wide trajectory, then freezes when it lands on ground) when approached by potential predators in general (Jackson & Hallas, 1986a), and wild leaps were also made when *Scytodes* spat toward *Portia*. *Portia labiata* (LB) was more likely (95%) than *P. labiata* (SL)(56%, $P < 0.01$) to perform wild leaps if *Scytodes* spat.

Also, *P. labiata* (LB) sometimes escaped, after the *Scytodes* spat, by leaving behind a glued-down leg. *Ligurra* and *J. queenslandica*, however, were never seen to lose a leg to escape from *Scytodes*.

Discussion

Among the salticids studied, the three *Portia* were more efficient than *Ligurra* at circumventing *Scytodes*' special defence (spitting) and preying on this spider, and *P. labiata* (LB) was the most efficient of the *Portia*. *Portia* used aggressive mimicry, whereas *Ligurra* usually attacked by leaping into webs. It is interesting that *J. queenslandica* never invaded *Scytodes*' webs and attacked *Scytodes*. *J. queenslandica* is known to catch spiders by leaping or walking their webs, but the webs *J. queenslandica* invades are most often those of *Psilochorus* (Pholcidae) and *Inola subtilis* (Pisauridae) built on tree trunks and boulders (Jackson, 1988). Perhaps the web of *Scytodes* is not of a type that is of interest to *J. queenslandica*, and generally webs on leaves are probably not the kind of webs in which *J. queenslandica* is interested.

Aggressive mimicry appears to be an important factor in *Portia*'s greater success, compared with *Ligurra*, at circumventing the defence of, and preying on, *Scytodes*. However, although aggressive mimicry may tend to be the best overall strategy for an aggressive mimic (Whitehouse, 1986), its use alone does not guarantee that *Portia* will overcome *Scytodes*' defence. Instead, it appears to be critical that particular tactics of signalling are used. In particular, vibrating the web by consistently fluttering alone or by fluttering and striking together with palps appears to put *Portia* at considerable risk of being killed by the *Scytodes*: this was the signalling tactic often used by *Portia fimbriata* (Q) and *P. fimbriata* (Q) more often elicited spitting by *Scytodes* and was less efficient at catching *Scytodes* than *P. labiata* (LB). However, *P. labiata* (LB) more often used a signalling tactic of plucking with palps alone than did *P. fimbriata* (Q) or *P. labiata* (SL) and this tactic appeared more effective against *Scytodes*. Apparently, *P. labiata* for Los Banos, but not *Portia* from other places (*e.g.*, Queensland and Sri Lanka), has evolved, as a local adaptation, a *Scytodes*-specific pre-programmed tactic for precisely controlling the behaviour of *Scytodes*, a locally abundant prey in Los Banos.

However, there was more to the strategy of *P. labiata* (LB) than this. After

first using this signalling tactic, *Portia* frequently made detours before attacking. Jumping spiders have been reported previously to take simple detours to reach prey (Heil, 1936; Crome, 1957; Hill, 1979), apparently an ability related to these spiders' unique, complex eyes and acute vision (Land, 1974, 1985; Blest, 1985). Also, for *Portia*, detouring ability may be especially advantageous and recent studies indicate that the *Portia* tested (*P. fimbriata* (Q), *P. labiata* (SL) and *P. labiata* (LB)) readily undertake detours before attacking prey in both the field and laboratory, including long detours during which the prey can not be seen (Jackson & Wilcox, 1993a; Tarsitano & Jackson, 1992, 1994). The detours observed in the present study were not especially long or complex, and there was no uncrossable physical barrier that made detours a necessary. Instead, the detours seen in this study appear to be a compensation for the spitting behaviour of the unique prey. It is in the *Portia* that is sympatric with this unique prey that this compensation appears most pronounced: *P. labiata* (LB) was more likely than *P. fimbriata* (Q) and *P. labiata* (SL) to make a detour to a better ventage point for before leaping onto *Scytodes*, and *P. labiata* (LB) was more successful at catching *Scytodes* than *P. fimbriata* (Q) and *P. labiata* (SL).

The key to the success of *P. labiata* (LB) appears to be reliance on aggressive mimicry-detour-leap sequences. There are species of *Scytodes* found in the habitats of *Portia* in other places besides Los Banos. However, compared with Los Banos, *Scytodes* spp. are not so abundant either in Queensland where *P. fimbriata* lives or in Sri Lanka where *P. labiata* lives. Apparently, *P. labiata* (LB) has evolved a special pre-programmed behaviour for this unusual and especially dangerous prey.

The results from this study are consistent overall with those from previous studies on other species of web-builders: (1) *Scytodes* has a defence behaviour which provides a degree of protection against web-invading predators; (2) web-invading salticids that use aggressive mimicry tend to be more effective than other salticids at overcoming *Scytodes*'s defence and catching this spider. However, in contrast to the previous studies (Jackson, 1990c; 1992c, d, e), the present study reveals that *P. labiata* (LB), the spider which is the most consistent in detouring when pursuing *Scytodes* before attacking, but not *P. fimbriata* (Q),

the spider which is the most consistent in using aggressive mimicry, is the most efficient at catching *Scytodes*. There appears to have been evolutionary fine tuning of *P. labiata* (LB)'s strategy to this unusual prey.

CHAPTER 8

Fine tuning of prey preference of *Portia labiata*, an araneophagic jumping spider (Araneae: Salticidae), for a spitting spider, *Scytodes* sp. indet. (Araneae: Scytodidae) from the Philippines

Abstract: *Portia labiata* routinely feeds on *Scytodes* sp. indet., a spitting spider (Scytodidae), in nature in Los Banos, the Philippines, and also uses *Scytodes*-specific capture behaviour (aggressive mimicry-detour-leap sequence) for catching this unusual and especially dangerous prey in the laboratory. In the present study, fine tuning of prey preferences of Los Banos *P. labiata* related to whether *Scytodes* is brooding was studied by using three types of tests of prey preference in the laboratory conditions. Consistently across three types of tests, the Los Banos *P. labiata* preferred brooding *Scytodes* over non-brooding *Scytodes* as prey. *P. labiata*'s prey preference did not vary with hunger level. Also, the same preference determined from tests using living, active prey was also found in tests using dead, motionless lures: evidently *P. labiata* can discriminate between different types of prey independent of their movement patterns.

Introduction

The Salticidae is a large family of spiders (Prószyński, 1971; Coddington & Levi, 1991) in which selective foraging is especially likely. These spiders have unique, complex eyes and acute vision (Land, 1969a, b; 1974; 1985; Forster, 1982a; Blest *et al.*, 1990) which enable them, prior to contact, to discriminate between different types of prey (Jackson & Blest, 1982b; Jackson & Tarsitano, 1993; Jackson, 1995; Wilcox, *et al.*, 1996).

Especially pronounced predatory versatility is known in two groups of jumping spiders, myrmicophagic (ant-eating) species (Richman & Jackson, 1992; Chapter 2 & 3) and araneophagic (spider-eating) species (Jackson, 1992a). The prey (ants and spiders) of myrmicophagic and araneophagic salticids are both unusual and potentially dangerous, and the prey-specific capture behaviour of the

species in each of these two salticids groups appear to be critically important in enabling them to be effective at catching these special prey.

In myrmicophagic salticids, not only has prey-specific capture behaviour evolved; also, these salticids prefer ants to other insects (Jackson & van Olphen, 1991, 1992; Chapter 2 & 3). Parallel findings have come from studies of araneophagic salticids (Chapter 4 & 5).

In *Portia*, behaviour repertoires vary among species and even among populations of single species. In particular, the habitat in which *Portia fimbriata* lives in Queensland appears to be unique among those studied in having an especially high abundance of cursorial salticids (Jackson & Hallas, 1986a) and the Queensland *P. fimbriata* has a prey-specific capture behaviour for this locally abundant type of prey (Jackson, 1992a). The Queensland *P. fimbriata* also prefers salticids to other spiders as prey (Chapter 4). Apparently, both prey-specific capture behaviour and prey-preference have been shaped in a fine-grain manner to the kind of prey that is locally abundant (Chapter 10).

In the present chapter, a different kind of fine tuning will be considered: preference for brooding over non-brooding females of a particularly dangerous prey species. In this study, the predator is *Portia labiata*, prey is *Scytodes* sp., and the habitat is Los Banos (the Philippines).

Portia labiata has a range that extends through tropical Asia (Wanless, 1984). However, *P. labiata* in Los Banos (in the Philippines) frequently feeds on a locally abundant and unusually dangerous prey-spider species, *Scytodes* sp. indet., a web-building spitting spider that feeds especially on cursorial salticids that abound on the same leaves where it builds its web (Chapter 6). *P. labiata* from Los Banos itself is a salticid that uses *Scytodes*-specific capture behaviour to feed on this salticid-eating spider (Chapter 7).

The distinction between brooding and non-brooding *Scytodes* may be important for two reasons. All species of *Portia* studied eat spider eggs. When *P. labiata*'s prey is a brooding *Scytodes*, *P. labiata* gets both the eggs and the spider as prey. Also, a brooding *Scytodes* can be expected to be a safe prey because *Scytodes* has a special maternal behaviour: females carry egg sac in their chelicerae. Because *Scytodes*' spit comes out of the chelicerae, a brooding

Scytodes female is temporarily disarmed: she can spit only by first releasing her eggs.

The present chapter is a study of whether *P.labiata* prefers brooding or non-brooding *Scytodes*? Are preferences of *P. labiata* hunger-driven? Does *P. labiata*'s preference depend on cues from the prey's different movement patterns?

Materials and methods

General

Laboratory cultures of *P. labiata* and *Scytodes* were established from spiders collected in Los Banos (the Philippines). Maintenance procedures, cage design, basic testing methods and terminology were as in earlier salticid studies (Jackson & Hallas 1986a; Jackson & van Olphen, 1991, 1992; Chapter 4 & 5), and only essential details are given here. Lights came on in the laboratory at 0800 h and went off at 2000 h. Each test was carried out between 0900 h and 1700 h.

All individual *P. labiata* were fed only house flies (*Musca domestica*) prior to testing. 'Well-fed' and 'starved' *P. labiata* were kept without food for 7 and 15 days, respectively, prior to testing. Unless stated otherwise, all *P. labiata* were well fed. All *P. labiata* tested were adult females (body length: 8-10 mm). All *Scytodes* (or *Scytodes* plus eggs) used as prey and lures were about half the body size of the *P. labiata* ('small': see Chapter 4). Both brooding and non-brooding *Scytodes* were always in webs. The webs were built by *Scytodes*, which were put into cells 5 days prior to a test.

Tests of prey preference using living Scytodes

As in Chapter 4, tests with living prey were carried out in a prey preferences testing box (PPTB: Fig. 1 in Chapter 4) made from plastic and consisting ten cells (each cell 80 X 80 X 20 mm). The top of the apparatus was transparent, but the sides of each cell were opaque so that a *P. labiata* in one

cell could not see into neighbouring cells. Before testing began, one of two tubes connected to each cell held a *P. labiata*; and the distal end of every tube was stoppered by the tips of the teeth of the 'comb'. The second tube on each cell was empty before and during Type 1 & 2 tests (see below). In Type 3 tests, a cage made from petri dish (90 mm in diameter) was used (see below).

In Type 1 & 2 tests, the *P. labiata* was first placed in one of the two tubes. To begin testing, screens between the tubes and cells were removed and the combs were pushed in slowly, forcing each of ten *P. labiata* into one of the ten cells. Once the *P. labiata* entered the cells, the screens were replaced (for details, see Chapter 4).

The test ended when the *P. labiata* captured a prey or 30 min elapsed, whichever came first, except that observations continued until the sequence ended if the *P. labiata* was pursuing a prey when the 30-min period elapsed. No individual *Portia* was used in more than one test of any one type.

In Type 1 test, one *Scytodes* was put into each cell first 10 minutes before the *P. labiata* was allowed to enter. In Type 2 tests, two *Scytodes*, one brooding and the other not, were put into each cell 10 minutes before the *P. labiata* was allowed enter.

Tests for prey preferences of well-fed P. labiata

Two prey types (brooding *Scytodes* and non-brooding *Scytodes*) and three testing methods were used.

A. *Does P. labiata prefer brooding or non-brooding Scytodes?*

1. *Type 1 tests (one individual of one prey type presented to a P. labiata at a time on alternate days)*

Each *P. labiata* was used in a pair of tests (one individual of one type of prey on one day and one individual of the other type on the following day). Half of the *P. labiata* was tested first with brooding *Scytodes*; the other half was tested first with non-brooding *Scytodes*. Each *P. labiata* was assigned to one of the two groups randomly. Each *Scytodes* (or *Scytodes* plus eggs) was in its own web.

2. *Type 2 tests (two types of prey presented to a P. labiata simultaneously; one individual prey of each type)*

Each test began when a *P. labiata* was allowed to enter a cell containing one brooding *Scytodes* and one non-brooding *Scytodes*, both being in the same web built by one of the two *Scytodes*, and ended when the *P. labiata* took one of the two *Scytodes* (*i. e.*, it was not allowed to take both).

3. *Type 3 tests (P. labiata feeding on one prey type presented with alternative prey type)*

A *P. labiata* was given access to a brooding *Scytodes* while feeding on a non-brooding *Scytodes* on one day; on the alternate day, the same *P. labiata* was given access to a non-brooding *Scytodes* while feeding on a brooding *Scytodes*. Half of the *P. labiata* tested fed on a non-brooding *Scytodes* and half on a brooding *Scytodes* in the first test (decided randomly).

Scytodes (with or without eggs) were housed in 90-mm-diameter cages made from a plastic petri dishes, and allowed to build webs. To begin a test, a *P. labiata* was allowed to enter a cage containing a *Scytodes* in a web (with or without eggs). The *P. labiata* was first placed in a transparent plastic tube (10 mm in diameter); within 5 min, one end of the tube was connected to a hole in the bottom of the cage and the other end was plugged with a cork. The *P. labiata* could enter the cage by walking up out of the tube and usually did so within 5 min. Once the *P. labiata* entered the cage, the tube was removed and the hole in the cage was plugged with a cork. If the *P. labiata* began eating the insect within 30 min, the cover of the cage, with the feeding *P. labiata* on it, was removed *c.* 15 min later; next, this cage cover was placed on another open cage in which there was a *Scytodes* (without or with eggs; opposite of *Scytodes* on which *P. labiata* was feeding) in its web.

If *P. labiata* did not capture and begin feeding on the first prey within the allowed 60 min, the test was repeated on each succeeding day until it did so (maximum time that elapsed: 4 days).

B. *Tests for preferences of starved Portia*?

All the above tests carried out on well-fed *P. labiata* females were also carried out using starved *P. labiata*. Results from testing well-fed females were compared with results from testing starved females.

Tests of prey preference using motionless lures

Each lure was mounted on a cork and the lure plus cork was sprayed with an aerosol plastic adhesive for preservation and for elimination of potential odour cues from the dead spider and eggs (see Chapter 4). If *P. labiata* contacted the lure during a test, the lure was washed with 80% ethanol and allowed at least 24 h to dry before being using again.

One type of choice ramp (CR) was used: Type II (Fig. 3 in Chapter 4). Between each test, the ramp was wiped off with 80% ethanol, then allowed to dry for at least 30 min, to remove possible chemical traces from *P. labiata* that had been on the ramp in earlier tests.

The Type II CR was Y-shaped, but each arm ended at a wall holding a plastic petri dish containing a *Scytodes* web. Petri dishes were open during tests. For a lure, a dead *Scytodes* (with or without eggs) was glued to a cork disk and positioned at the centre of an otherwise vacant web. Vacant webs were obtained by removing the host spiders 7 days before tests began and leaving the webs exposed during this 7-day period. (For details, see Chapter 4).

Before starting a test, the *P. labiata* was placed in the pit, and the pit was covered with a clear plastic cover until the *P. labiata* became quiescent. The cover was then removed to start the test.

The test was aborted if *P. labiata* stayed in the pit for 30 min or moved off the ramp to the line below where the two arms of the Y-shaped ramp joined. When tests were aborted, *P. labiata* was re-tested repeatedly, up to four times a day, then on subsequent days, until a successful test was completed or four days of unsuccessful testing elapsed.

P. labiata were chosen for tests at random from the laboratory cultures, and no individual *P. labiata* was used in more than one test of any one type. Successful tests ended when *P. labiata* did one of the following or 30 min

elapsed after *P. labiata* left the pit: 1) arrived at an arm on which no lure was present (applicable only to Type 1 tests, see below); 2) moved onto an arm and began to stalk the lure, but walked off the ramp arm before reaching the end; 3) moved onto an arm of the CR, then leapt off without attacking the lure; 4) moved onto an arm the CR, then reached the end and entered the web but did not signal; 5) arrived at an arm, then entered the web and signalled, but did not attack the lure; 6) arrived at an arm, stalked while still distant, then retreated by walking backward and moving off the arm of the ramp; 7) arrived at an arm, then entered the web, signalled and attacked the lure.

Terminology and the basics of testing procedure for lures were as when living prey were used. The equivalent of Type 1 & 2 tests with living prey were carried out using lures, but the equivalent Type 3 tests proved too difficult to perform with lures. All tests were carried out using both well-fed and starved *P. labiata* females.

Results

Tests for prey preference using living prey

In tests on alternate days (Type 1 tests), when only a single prey type was presented at a time, well-fed *P. labiata* attacked and ate brooding *Scytodes* more often than they attacked and ate non-brooding *Scytodes* (TABLE I).

In tests in which two prey were presented simultaneously (Type 2 Tests), well-fed *P. labiata* females attacked and ate brooding *Scytodes* first more often than they attacked and ate non-brooding *Scytodes* first (TABLE II).

In Type 3 tests, well-fed *P. labiata* dropped non-brooding *Scytodes* to take brooding *Scytodes* more often than they dropped brooding *Scytodes* to take non-brooding *Scytodes* (TABLE III).

TABLE I

Results from Type 1 tests (Portia labiata tested with one prey at a time on alternate days), showing that brooding Scytodes (prey 1) were attacked and eaten more often than non-brooding Scytodes (prey 2). Both types of prey were in webs

	Attacked (ate) prey 1 only	Attacked (ate) prey 2 only	Attacked (ate) both	Attacked (ate) neither	McNemar test[1]
Well-fed *P. labiata*	23 (21)	6 (5)	9 (7)	8 (13)	$P<0.005$ ($P<0.005$)
Starved *P. labiata*	17 (14)	6 (4)	4 (3)	3 (9)	$P<0.05$ ($P<0.05$)

[1] Data in first two columns only used in these tests

TABLE II

Results from Type 2 tests (two prey presented to Portia labiata simultaneously), showing that brooding Scytodes (prey 1) were attacked and eaten more often than non-brooding Scytodes (prey 2). Both types of prey were in webs

	Attacked prey 1 first (ate prey 1)	Attacked prey 2 first (ate prey 2)	Attacked neither (ate neither)	Test of Goodness of fit[1]
Well-fed *P. labiata*	26 (24)	8 (6)	10 (19)	$P<0.005$ ($P<0.005$)
Starved *P. labiata*	19 (17)	7 (6)	4 (7)	$P<0.05$ ($P<0.05$)

[1] Data in first two columns only used in these tests

TABLE III

Results from Type 3 tests (Portia labiata given second prey while feeding on first prey), showing that P. labiata dropped non-brooding Scytodes to take brooding Scytodes more often than they dropped brooding Scytodes to take non-brooding Scytodes. Both types of prey were in webs

	Drop prey 1 to attack prey 2	Drop prey 2 to attack prey 1	Drops each to attack other	Drops neither	McNemar test[1]
Well-fed *P. labiata*	2	18	1	29	$P < 0.001$
Starved *P. labiata*	3	13	0	14	$P < 0.001$

[1] Data in first two columns only used in these tests

Tests for prey preference using motionless lures

In tests on alternate days (Type 1 tests), when only a single lure was presented at a time, *P. labiata* chose lures made from brooding *Scytodes* more often than they chose lures made from non-brooding *Scytodes* (TABLE IV).

In tests with simultaneously presented lures (Type 2 tests), *P. labiata* chose *Scytodes* lures made from brooding *Scytodes* lures more often than lures made from non-brooding *Scytodes* lures (TABLE V).

Do starved and well-fed Portia prefer different prey?

In each type of test, both well-fed and starved Los Banos *P. labiata* females exhibited similar preferences.

TABLE IV

Results from Type 1 tests (Portia labiata tested with one lure at a time on alternate days), showing that brooding Scytodes (lure 1) were attacked more often than non-brooding Scytodes (lure 2). Both types of lures were in webs

	Chose lure 1 only	chose lure 2 only	chose both	chose neither	McNemar test[1]
Well-fed *P. labiata*	21	5	14	14	$P < 0.005$
Starved *P. labiata*	18	6	12	4	$P < 0.05$

[1] Data in first two columns only used in these tests

TABLE V

Results from Type 2 tests (two prey lures presented to Portia labiata simultaneously), showing that brooding Scytodes (lure 1) were attacked more often than non-brooding Scytodes (lure 2). Both types of prey were in webs

	Chose lure 1 first	Chose lure 2 first	Chose neither	Test of Goodness of fit[1]
Well-fed *P. labiata*	32	12	13	$P < 0.005$
Starved *P. labiata*	26	11	3	$P < 0.05$

[1] Data in first two columns only used in theses tests

Discussion

In nature, the Los Banos *Portia labiata* frequently preys on *Scytodes* sp., a salticid-eating spitting spider (Chapter 6). Also, the Los Banos *P. labiata* uses *Scytodes*-specific (*i.e.*, specialized) capture behaviour against this unusual and exceptionally dangerous prey in its diet (Chapter 7). The present study illustrates yet another way in which the Los Banos *P. labiata* is behaviourally specialized on *Scytodes*.

The Los Banos *P. labiata* takes brooding *Scytodes* in preference to non-brooding *Scytodes*. *Scytodes*' spit comes out of the chelicerae, but an egg-carrying (brooding) *Scytodes* female is temporarily disarmed, and therefore relatively safe for a *Portia*. This preference appears to be adaptive fine tuning of *P. labiata*'s prey preference behaviour that reduces the risk from this especially dangerous prey. That is, *P. labiata* appears to have evolved prey preference behaviour that enables it to make fine distinctions between subclasses of a dangerous prey, and thereby reduce the danger to which it is subjected.

Additionally, predation on brooding *Scytodes* gives *Portia* access to the eggs of its prey, and this may well be a food of especially high nutritive value (Jackson & Blest, 1982a).

Effects of hunger on the behaviour of predators (Curio, 1976), including salticids (Drees, 1952; Gardner, 1964) and other spiders (Punzo, 1989), are well known, but whether hunger affects the prey-preferences of salticids has received little attention prior to recent studies of myrmicophagic and araneophagic salticids. In *Corythalia canosa*, *Chrysilla lauta*, *Natta* spp. and *Siler semiglaucus* (Jackson & van Olphen, 1991, 1992), well-fed individuals prefer ants to other prey, but individuals of these species, when starved for 2 weeks prior to testing, appear to take ants and other insects indiscriminately. However, in *Habrocestum pulex* (Chapter 2), in *Chalcotropis* sp., *Euophrys* sp. 1 and 2, *Siler* sp. and *Telamonia* (Chapter 3), another 6 species of myrmicophagic salticid, and in araneophagic *Portia* studied (Chapter 4 & 5), there is no evidence that a prior

period of two weeks without food affects prey preferences. Data from the present paper indicate that Los Banos *P. labiata* resembles other *Portia* studied: a two-week period without food had no noticeable effect on the type of preference studied (starved *P. labiata* still took brooding *Scytodes* in preference to non-brooding *Scytodes*).

Prey movement is an especially effective in stimulating salticids to orient toward and pursue prey (Drees, 1952; Dill, 1975). Also, cues from different styles of movement are sometimes used by salticids to distinguish between different types of prey (Freed, 1984). However, cues from prey movement are not always necessary. Salticids sometimes stalk and attack motionless prey (Forster, 1985; Jackson & Tarsitano, 1993), and *Portia*, in particular, routinely preys on quiescent web-building spiders (Jackson & Hallas, 1986a). On the basis of visual cues alone, *Portia* can distinguish between quiescent spiders, insects and eggsacs (Jackson, 1995; Wilcox *et al.*, 1996) and *Portia* uses the same prey-specific capture behaviour against different kinds of motionless prey as they normally use against the same kinds of living prey (Jackson & Tarsitano, 1993). Furthermore, when tested using dead, motionless prey, Kenya *P. africana* and *P. schultzi*, Queensland *P. fimbriata* and Sri Lanka *P. labiata* showed the same preferences as in tests using living prey (Chapter 4 & 5). Evidently, cues from prey shape alone are sufficient for eliciting *Portia*'s preferences for different taxonomic categories of prey.

In this chapter, Los Banos *P. labiata* had the same preferences when tested with dead, motionless lures as when tested with living, motile prey, when the prey and lures were brooding and non-brooding *Scytodes*. That is, *P. labiata* can distinguish brooding from non-brooding *Scytodes* on the basic of static visual cues alone.

SECTION V

EFFECT OF PREFERRED DIET ON FITNESS

CHAPTER 9

Influence of preferred diet on survivorship and growth in *Portia fimbriata*, an araneophagic jumping spider (Araneae: Salticidae) from Queensland

Abstract: The influence of diet on survival rate and growth was investigated in Queensland *Portia fimbriata*, an araneophagic salticid spider. Newly-hatched spiderlings of *P. fimbriata* were divided into three groups, and reared on different diets, but otherwise under identical conditions: spiders only (SO), insects only (IO), and a mixture of spiders and insects (MSI). For each diet, a variety of spider and insect species were used, and the spider diets included as prey both cursorial salticid species and web-building species. Individuals on the IO diet did not survive past the 5th instar, but juveniles reached maturity when raised on the other two diets. Survivorship of *Portia* raised on the SO diet was significantly higher than that of *Portia* fed on the MSI diet. Diet treatment had a significant effect on body size dimensions measured at the 4th instars and at maturity. In addition, *P. fimbriata* reared on the SO diet reached sexual maturity significantly earlier than those reared on the MSI diet. These results suggest that there are fitness-related consequences of prey specialization in *P. fimbriata*, and these implications are discussed in relation to optimal foraging theory.

Introduction

A basic assumption underlying optimal foraging theory (OFT) is that predatory behaviour is shaped, directly or indirectly, by natural selection (Stephens & Krebs, 1986). Optimal diet theory (ODT), a branch of OFT, is an attempt to understand how preference (*e.g.*, of a predator for certain types of prey) maximizes the predator's fitness (Emlen, 1966; MacArthur & Pianka, 1966; Pyke *et al.*, 1977; Morse, 1980; Pyke, 1984; Schoener, 1987). However, modifications of OFT suggest that, besides net rate of energy intake, various other currencies may be important (Schoener, 1971; Pyke, 1984; Cheverton *et al.*, 1985), including the intake of particular essential nutrients (Goss-Custard, 1981; Kennish, 1996) and the intake of necessary or at least beneficial mixtures of nutrients (Eason, 1969; Westoby, 1978; Greestone, 1979; Nicotri, 1980; Pierotti

& Annett, 1987).

Predators that exploit specialized dietary regimes, use prey-specific capture behaviour against particular types of prey and also have preference for the targeted prey are of particular interesting. Are there advantages to feed on the targetted prey that can be expressed as components of fitness? A starting point might be to consider effects on survival and growth.

Some predictions from ODT (Pyke, 1984) may be especially important: 1) absolute preferences that depend on the abundance of the one better (preferred) prey type, rather than on the abundances of each of the various available types of prey, are expected when the predator's fitness depends absolutely on something it gains from only this one particular type of prey (*e.g.*, there may be an essential nutrient obtainable only from the preferred prey); 2) partial preferences are expected if fitness depends on the value of more than one type of food (*e.g.*, fitness might depend on both maximizing energy intake and on obtaining a mixture of nutrients, or fitness may depend on both mean and the variance of energy intake); 3) preferences that depend on the abundances of all types of prey, rather than on the abundances of just the better prey types, are expected when the predator's fitness depends on things it obtains from more than one type of food. Each of these three predictions imply that prey preferences have fitness consequences.

In the present study, I examine the influence of preferred diet on survivorship and growth in *Portia* Karsch, a genus of araneophagic jumping spiders (Salticidae)(Wanless, 1984). The capture behaviour of five species of *Portia* has been studied previously (Jackson, 1992a; Jackson & Pollard, 1996): *P. africana* (Simon) and *P. schultzi* Karsch from Kenya; *P. albimana* (Simon) from Sri Lanka; *P. labiata* (Thorell) from Malaysia and Sri Lanka; and *P. fimbriata* (Doleschall) from Australia, Malaysia, and Sri Lanka. Each of these species preys on spiders in nature by using prey-specific capture behaviour (vibratory aggressive mimicry). Each of these species of *Portia* also preys on insects (either in or out of webs), and the Queensland *Portia fimbriata* also preys frequently on spiders of its own family (*i.e.*, ordinary, insectivorous salticids). Experimental studies have shown that *P. africana*, *P. fimbriata*, *P. labiata* and *P. schultzi* prefer

spiders to insects as prey (Chapter 4 & 5). *P. fimbriata* is used in the present study.

Materials and methods

Cultures of *Portia fimbriata*, established from specimens collected in Queensland, Australia, were studied in the laboratory in Christchurch. As maintenance procedures, cage design, basic testing methods and terminology were as in earlier salticid studies (Jackson & Hallas, 1986a; Hallas, 1989), only essential details are given here.

Females that had matured and mated in the laboratory provided eggs for the study. These eggs were placed in an incubator (see Hallas, 1988) and, following hatching and dispersal, 'first instar' spiderlings (for definition, see Hallas, 1988) were isolated into plastic cages (5 X 5 X 7 cm) and assigned at random to the experimental groups. Water was supplied to the spider through a wet cotton roll, and leaf debris provided resting sites. The juvenile *Portia* were transferred to larger cages (15 X 10 X 5 cm) at instar 3 and again (25 X 25 X 25 cm) when 'subadult' (*i.e.*, in the instar immediately preceding maturity). Rearing conditions for all *Portia* were identical except for diet: 12L:12D light:dark cycle (lights came at 0800 h and went off at 2000 h), constant 25°C temperature, and constant relative humidity (80%).

Feeding rate was three times a week. Species of spiders used for the laboratory diet (TABLE I) were collected either in Queensland or locally. Three diets were used: 1) spiders only (SI)(mixture of species, including both cursorial salticid spiders and web-building spiders); 2) insects only (IO)(mixture of various insect species); and 3) mixed diet (MSI) consisting of both all of the kinds of spiders used for SO diet and all of the kinds of insects used for IO diet. Prey were always about half the size of the *Portia*. By using juveniles (spiderlings) of the prey, appropriate size could be provided. At each feeding, 3-5 individual prey spiders (SO) or insects (IO) were provided. For *Portia* on a mixed diet (MSI), 3-5 individual prey items (spiders or insects) were provided each time, with alternate feedings being spiders only or insects only.

TABLE I

Prey used in the laboratory for rearing Queensland Portia fimbriata

Species	Order	Family	Description	Body length of adult (mm)	Origin
Achaearanea sp.	Araneae	Theridiidae	Web-building theridiid spider	1 - 5	New Zealand
Badumna longinqua (L. Kock)	Araneae	Amaurobiidae	Web-building spider	1 - 10	New Zealand
Tegenaria domestica (Clerck)	Araneae	Agelenidae	Web-building agelenid spider	1 - 5	New Zealand
Zosis geniculatus (Oliver)	Araneae	Uloboridae	Web-building uloborid spider	1 - 5	Queensland
Euophrys parvula (Bryant)	Araneae	Salticidae	Cursorial salticid	1 - 7	New Zealand
Jacksonoides queenslandica Wanless	Araneae	Salticidae	Cursorial salticid	1 - 7	Queensland
Marpissa marina Goyen	Araneae	Salticidae	Cursorial salticid	1 - 6	New Zealand
Trite planiceps (Urquhart)	Araneae	Salticidae	Cursorial salticid	1 - 8	New Zealand
Ctenopseustis sp.	Lepidoptera	Tortricidae	Moth	4 - 6	New Zealand
Melancha sp.	Lepidoptera	Noctuidae	Moth	6 - 8	New Zealand
Macrosiphum euphorbiae (Thomas)	Hemiptera	Aphidae	Aphid	1 - 2	New Zealand
Drosophila immigrants (Sturtevant)	Diptera	Drosophilidae	Fruit fly	3 - 4	Lab. culture
Drosophila melanogaster (Meigen)	Diptera	Drosophilidae	Fruit fly	1 - 2	Lab. culture
Macromastix zeylandia Alexander	Diptera	Tipulidae	Crane fly	5 - 6	New Zealand
Musca domestica (Linnaeus)	Diptera	Muscidae	House fly	4 - 8	Lab. culture
Trichocera annulata (Meigen)	Diptera	Trichoceridae	Crane fly	4 - 6	New Zealand

All insects: adults. Spiders: juveniles and adults

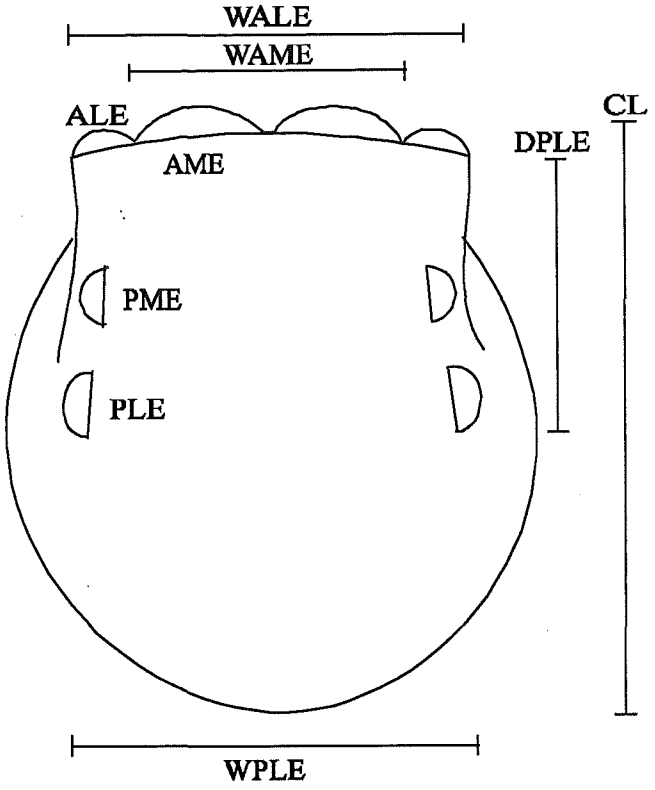

Fig. 1. Carapace of *Portia fimbriata*. Bars indicate measurements taken off each spider in each instar and growth. ALE: anterior lateral eyes. AME: anterior medial eyes. PLE: posterior lateral eyes. PME: posterior medial eyes. CL: carapace length. DPLE: distance between ALE and PLE. WAME, WALE and WPLE: distances between outside margins of AME, ALE and PLE, respectively.

P. fimbriata's survival was monitored until sexual maturity. For each experimental diet, survival rate was calculated for each instar and for the total juvenile period. Per-instar survival was calculated as the percentage of those individuals in the preceding instar that survived to the next instar. Total-juvenile

survival was the percentage of the total numbers of individuals (*i.e.*, in the numbers in the initial instar at the start of the study) that reached maturity.

Discarded exuviae were collected 24-48 h after each moult, and instar duration (the time elapsing between successive moults) was recorded. Exuviae and all individuals that reached maturity from each experimental group were also measured. Body length (BL) and five carapace dimensions (Fig. 1), measured with an ocular micrometer, were used as indicators of size.

Statistical tests used are from Sokal & Rohlf (1981).

Results

Age-specific mortality

In insects, the number of instars necessary to reach maturity tends to be more or less constant for a species (Ratte, 1985). However, the number of juvenile instars usually varies intraspecifically in spiders (Foelix, 1982). In the present study, as shown previously by Hallas (1989), Queensland *P. fimbriata* reached maturity at instar 7, 8, or 9.

A life table (TABLE II) was made by calculating the cumulative proportion of individuals surviving at the beginning of each instar (Fig. 2) and the mortality rate per instar (the proportion of individuals from the previous instar that died). When raised on a diets of spiders only (SO), mortality rates peaked in instar 6. When reared on a diet of insects only (IO), mortality rates peaked at instar 5, and no individuals entered instar 6. When reared on a mixed diet of spiders and insects (MSI), the instar in which *P. fimbriata* suffered its highest mortality rates was highly variable, and there was no clear tendency for mortality to become greater or lesser over successive instars.

Survivorship per instar varied significantly between the three different diets (Kolmogorov-Smirnov tests; SO diet *vs.* IO diet: $P < 0.0001$; SO diet *vs.* MSI diet: $P < 0.01$; MSI diet *vs.* IO diet: $P < 0.001$).

TABLE II

Summary of life history data for Portia fimbriata reared on three diets: spiders only (SO), insects only (IO), and mixed of spiders and insects (MSI). N: No. of individuals entering an instar. lx = cumulative survivorship. qx = mortality rate.

		Juvenile instar								
Diet treatment		1	2	3	4	5	6	7	8	9
Insects only (IO)	N	88	76	71	63	34	0			
	lx	1.00	0.86	0.81	0.72	0.39	0.00			
	qx	0.14	0.07	0.11	0.46	1.00	-			
Spiders only (SO)	N	50	50	45	43	40	40	37	18	6
	lx	1.00	1.00	0.90	0.86	0.80	0.80	0.74	0.64	0.64
	qx	0.00	0.00	0.10	0.04	0.07	0.08	0.14	0.00	0.00
Mixed (MSI)	N	65	61	51	50	39	31	27	15	9
	lx	1.00	0.94	0.78	0.76	0.60	0.48	0.42	0.38	0.37
	qx	0.06	0.20	0.02	0.22	0.21	0.13	0.07	0.04	0.00

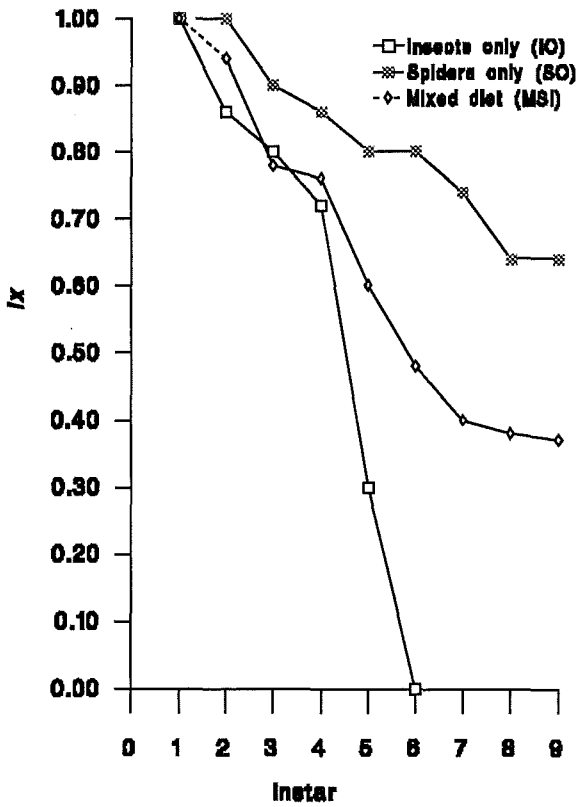

Fig. 2. Survivorship values (*lx*) of *Portia fimbriata* for successive instars reared on three different diets.

Survival to maturity

The percentage of spiders at the start of the study (*i.e.*, first instars) that subsequently survived to maturity (TABLE III) varied among treatments (diets): higher (test of independence: $X^2 = 8.29$, $P < 0.005$) on SO diet (64%) than MSI diet (37%), and also higher ($X^2 = 73.2$, $P < 0.001$) on SO diet than on IO diet (0%).

TABLE III

Survival to maturity as a percentage of total No. of first instars reared under each of three diet treatments

Diet treatment	Number initially in 1st instar	No. of adults obtained			Percentage to reach maturity
		Females	Males	Total	
Insects only (IO)	88	0	0	0	0
Spiders only (SO)	50	18	14	32	64
Mixed (MSI)	65	14	10	24	37

Maturation time

When analysing data on maturation time, data from individuals fed on a diet of insects only (IO) were excluded because, under this treatment, *P. fimbriata* did not survive past the 5th instar and none reached maturity. *P. fimbriata* raised on the SO diet reached sexual maturity earlier than *P. fimbriata* raised on the MSI diet (SO diet, mean ± SD of 217 ± 21 days; MSI diet, 245 ± 17 days)(one-way ANOVA: $F = 13.63$, $n = 31$, $P < 0.001$).

Body size

Body size parameters could be measured for the juvenile instars only for individuals fed on a diet of insects only (IO) because none reached maturity. All

instars (including adults) under the other two diet treatments were measured. Body size data from adult males are not presented here as sample size of adult male exuviae collected was small (for SO diet: 4; for the MSI diet: 3). *P. fimbriata* females at maturity were larger in all measures when raised on the SO diet than when fed on the MSI diet (TABLE IV).

When comparing different diet treatments for the fourth instar (TABLE IV), juveniles raised on the SO diet were significantly larger, in all six body-size parameters, than juveniles on the IO diet. Also, juveniles on the SO diet were, in CL, WPLE and WAME, larger than juveniles on the MSI diet; however, there were no evident differences between SO and MSI in BL, WALE and WPLE. Body size measures of juveniles raised on the IO diet differed from those of juveniles on the MSI diet only for BL and CL.

TABLE IV

Mean ($\bar{x}$) and standard deviation (SD) for body length and 5 carapace measurements (see Fig. 1) of Queensland Portia fimbriata fed on different diets

	Body size parameters of 4th instar juveniles						Body size parameters of adult females					
	BL	CL	WPLE	WAME	WALE	WPLE	BL	CL	WPLE	WALE	WAME	DPLE
Insects only (IO)												
$\bar{x}$	2.75	1.69	1.09	1.18	0.83	0.77						
SD	0.02	0.04	0.09	0.04	0.02	0.02						
n	24	24	24	24	24	24						
Spiders only (SO)												
$\bar{x}$	3.585	1.81	1.16	1.23	0.84	0.80	10.0	4.01	2.72	2.867	2.06	1.34
SD	0.122	0.04	0.06	0.02	0.01	0.02	0.41	0.13	0.03	0.036	0.12	0.05
n	23	23	23	23	23	23	14	14	14	14	14	14
Mixed (MSI)												
$\bar{x}$												
SD	3.57	1.77	1.13	1.19	0.84	0.79	9.16	3.83	2.70	2.813	1.88	1.27
n	0.13	0.05	0.03	0.05	0.02	0.02	0.33	0.05	0.03	0.024	0.04	0.07
	20	20	20	20	20	20	10	10	10	10	10	10
t-test												
SO *vs* MSI *P*-value	NS	0.05	0.05	0.01	NS	NS	0.001	0.001	0.05	0.005	0.005	0.05
SO *vs* IO *P*-value	0.001	0.001	0.005	0.001	0.05	0.005						
IO *vs* MSI *P*-value	0.001	0.005	NS	NS	NS	NS						

Discussion

In nature, the predominant prey of *Portia fimbriata* appears to be spiders (Jackson & Blest, 1982a; Jackson & Hallas, 1986a; Jackson, unpubl. data). By using prey-specific capture behaviour against spiders, *P. fimbriata* is efficient at catching this unusual type of prey (Jackson & Hallas, 1986b). *P. fimbriata* is also behaviourally specialized in another way: it has a distinctive behaviour of preferring spiders (both web-building spiders and cursorial salticid spiders) to insects (Chapter 4).

The present study provides evidence that feeding on the preferred prey has important effects on *P. fimbriata*'s development rate, body size at maturation and, especially, survival: when fed on preferred prey (*i.e.*, spiders only), most individuals of *P. fimbriata* survived to reach maturity, but no individuals survived past the 5th instar when fed on less preferred prey (*i.e.*, insects only). Also, on a diet of spiders, *P. fimbriata* developed faster and obtained larger size body when mature. When fed on a mixture of more preferred prey (spiders) and less preferred prey (insects), surviving individuals developed more slowly and obtained smaller size at maturity than was the case for individuals on a spiders-only diet; however, most individuals on the mixed diet died before reach maturity.

From a number of previous studies, it is shown that spiders, especially wolf spiders (Lycosidae), often die before maturing when raised on a diet composed of only one species of prey (Miyashita, 1968; van Dyke & Lowrie, 1975; Riechert & Harp, 1987; Uetz *et al.*, 1992). However, the present study was different because *P. fimbriata* received a variety of prey species under each diet.

Earlier studies suggest that critical nutrients for the spider may be absent from certain prey species. The best evidence for this is from lycosids which are known to suffer high mortality when fed on a diet of only fruit flies, *Drosophila melanogaster*, apparently because this insect lacks linoleic and linolenic acid, which are nutrients lycosids require (Uetz *at al.*, 1992).

Diet requirements may be more complex in some species. There is preliminary evidence that lycosids, by feeding on a mixture of prey, obtain an

optimal balance of nutrients (Greenstone, 1979). Also, laboratory-cultured prey may lack critical nutrients required by spiders even when the same prey species in the field is adequate: *Achaearanea tepidariorum* (C.L. Koch)(Theridiidae) had poor survivorship when fed mealworms whose diet was limited to standard mealworm bran; however, when mealworms were fed vitamin-enriched commercial bran cereals, spider survivorship was improved dramatically (Walcott, 1963).

The present study suggests that spiders as prey contain nutrients that are critically important for *P. fimbriata*. The flipside of this hypothesis is that *P. fimbriata* does not prefer insects because insects lack nutrients that are critical for survival and development. However, in the present study, the detrimental effects of feeding on insects were unlikely to be a consequence of the insects used being laboratory cultured because the insects used included both laboratory-cultured (*i.e.*, fruit fly and house fly) and field-collected species (*i.e.*, aphid, moth and crane fly).

Possibly in *P. fimbriata*, as may be the case in lycosids (Greenstone, 1979), a mixed diet is important as a means of getting an optimal mixture of different nutrients. However, the mixture that matters does not appear to be a mixture of spiders and insects: the MSI diet, compared to the SO diet, had detrimental, not beneficial, effects on *P. fimbriata*'s development. Whether *P. fimbriata*'s development would be adversely affected by a diet of a single prey-spider species has not been investigated. However, *P. fimbriata* preys on a large variety of spider species in nature by using a combination of pre-programmed and derived (by trial and error) prey-specific capture behaviours (Jackson & Wilcox, 1990, 1993a; Jackson & Pollard, 1996), suggesting that a diet based on mixing spider prey species may be important for this predator.

Higher survival rates, earlier maturity and larger size body at maturity by *P. fimbriata* with access to the preferred prey (spiders) appear to indicate important fitness consequences of dietary and behavioural specialization. The detrimental consequences of a diet of non-preferred prey (insects only, IO) on survival were particularly dramatic: no individuals reached maturity.

In three species of *Portia* (*P. fimbriata*, *P. labiata* and *P. schultzi*), females

of larger body size have larger batches of eggs and larger individual eggs than do smaller females (Hallas, 1987), and this trend is known for other spiders (Galiano, 1971; Kessler, 1971; Wise, 1979; Workman, 1979; Morse, 1980; Austin, 1984) and many other animal groups (Enders, 1976; Fenwich, 1984; Stearns, 1984). Although not investigated in *Portia*, it is also well known that larger spiders tend to win contests with smaller conspecifics over territory and mates (Austad, 1983; Chritenson, 1984; Suter & Keiley, 1984; Riechert, 1986; Uetz & Hodge, 1990; Whitehouse, 1991; Jackson & Cooper, 1991).

Early maturity may be important because spiders maturing early in the breeding season might have greater access to potential mates (Vollrath & Parker, 1992) and have a longer time to feed before laying eggs. In addition, offspring of the spiders that breed earlier might have a competitive size advantage over other broods, and might even cannibalize them (see Edgar, 1969). Although a diet of insects is detrimental for *P. fimbriata*, insects appear to be the standard prey of most salticid species. For example, the same insects used in the present study have been used routinely and successfully in the Canterbury spider laboratory to rear a wide variety of salticid species (Jackson, 1992b). Also, because *P. fimbriata* has been observed routinely to feed on the insects provided, the detrimental effects on *P. fimbriata* cannot be explained as a consequence of failure to catch and eat insects.

If *P. fimbriata* is metabolically specialized on spiders as prey, then *P. fimbriata*'s preference for spiders over insects is understandable, but other questions arise. Are there nutrients uniquely present in spiders on which *P. fimbriata* has become metabolically specialized? If so, studies are needed to clarify their biochemical identity. Also, how it is that a predator might have become metabolically dependent on nutrients uniquely available in certain prey is puzzling. Perhaps an advantage of metabolic specialization is being able to simply enzymatic systems and biochemical pathways, but, if so, there appears to be a price to pay (trade-off): a sacrifice in the ability to metabolize standard prey (insects).

Portia africana, *P. labiata* and *P. schultzi* resemble Queensland *P. fimbriata* by preferring spiders over insects as prey (Chapter 5), but for these

species of *Portia* the potential fitness consequences of diet need to be clarified. Also, there are other genera of araneophagic salticids (Jackson & Pollard, 1996), plus araneophagic spider species in another families (Jackson, 1992a), and little is known about the preference behaviour, much less the consequences of diet, in these species. However, a working hypothesis is that all araneophagic salticids are metabolically specialized on spiders as prey.

In common with araneophagic *Portia*, myrmicophagic salticids have prey-specific capture behaviour and preference for a prey (ants) that is avoided by most salticids (Jackson & van Olphen, 1991, 1992; Chapter 2 & 3), and the consequences of diet need to be studied in these species. There are, in addition to the myrmicophagic salticids, myrmicophagic spiders in other spider families (Hingston, 1928; Mathew, 1954; Harkness, 1977; Oliveira & Sazima, 1984, 1985, Harkness & Harkness, 1992), but the preferences of these spiders have not been examined in detail, and virtually nothing is known about the fitness consequences of diet in these species.

SECTION VI

DISCUSSION

CHAPTER 10

Prey-specific capture behaviour and prey preferences of myrmicophagic and araneophagic jumping spiders (araneae: salticidae)

Abstract: As prey for salticids, ants and spiders both can be dangerous. Not surprisingly, these dangerous prey appear not to dominate the diet of most salticid species. However, an interesting minority of salticid species routinely preys on either ants ('myrmicophagic salticids') or spiders ('araneophagic salticids'). I review recent work on two facets of behavioural specialization in myrmicophagic and araneophagic salticids: prey-specific capture behaviour and prey preferences. I suggest that predators evolving prey-specific capture behaviour against dangerous prey also tend to evolve distinctive preferences for these dangerous prey. Exceptionally acute eyesight, made possible by the unique, complex eyes of salticids, has probably facilitated the evolution of pronounced prey-specific capture behaviour and prey preferences in these spiders.

Introduction

The Salticidae is a large (over 4000 described species) and diverse family of spiders (Coddington & Levi, 1991) with unique, complex eyes and acute vision (Land, 1969a, b; Blest *et al.*, 1990). The typical prey of salticids tend to be soft-bodied, more or less safe insects such as flies, and acute vision probably enables salticids to avoid contacting potentially dangerous prey. However, in this paper, I consider salticids that specialize on potentially dangerous ants and spiders (Nentwig, 1986), prey that are rarely dominant in the diet of most salticid species. However, an interesting minority of salticid species routinely preys on either ants ('myrmicophagic salticids') or spiders ('araneophagic salticids') (Richman & Jackson, 1992). In the present paper, I review recent work on two facets of behavioural specialization in myrmicophagic and araneophagic salticids: prey-specific (*i.e.*, specialized) capture behaviour and prey preferences. However, because the term 'specialized' has been applied to both a predator's diet and its

predatory behaviour, it is important to first specify how the term 'specialized' is used here.

Stenophagous versus euryphagous predators

The diets of predators are often described as stenophagous or euryphagous and as specialized or generalized, where the terms 'stenophagous' and 'euryphagous' refer to the breadth of food resource utilization (*e.g.*, Morse, 1971; Fox & Morrow, 1981). Predators are considered to be stenophagous if their diets include only a narrow range of prey types (one or a few) and euryphagous if their diets include a wide range of prey types. It is useful to use 'stenophagous versus euryphagous' to refer to the predator's diet and 'specialized versus generalized' to refer to the predator's behaviour (see Jackson & van Olphen, 1991, 1992).

Predators with prey-specific capture behaviours are behaviourally specialized. A stenophagous predator may or may not have evolved prey-specific ('specialized') capture behaviour for use against the few types of prey in its diet. An euryphagous predator might be 'specialized' or 'generalized' in capture behaviour. That is, an euryphagous predator may use generalized (unspecialized) capture behaviour against the numerous types of prey on which it normally feeds. Alternatively, an euryphagous predator may be 'versatile' (Curio, 1976): it might use a conditional predatory strategy consisting of a repertoire of disparate prey-specific capture behaviours, each adaptively fine-tuned to a different type of prey in its broad diet. A versatile predator is, therefore, euryphagous in diet but behaviourally a specialist on multiple prey types.

An additional distinction is based on preference for prey types. A predator's prey preference is distinct from its actual diet and also from its capture behaviour. Preference, which implies ability to distinguish between different types of prey and choose one rather than another, cannot be inferred simply from knowing the animal's diet in nature or from knowing that the animal has prey-specific capture behaviour.

Specialization in the Salticidae

Spiders as a group are generally envisaged as more or less euryphagous in diet (Bristowe, 1941; Foelix, 1982; Wise, 1993). Yet, scattered reports in the literature (see Nentwig, 1986) suggest that stenophagy, prey-specific capture behaviour and distinctive preferences for unusual prey may be common. The present review is restricted to the Salticidae, a family that has two groups of species with especially pronounced predatory versatility - ant-eating (myrmicophagic) species and spider-eating (araneophagic) species (Richman & Jackson, 1992).

Detailed information about diet, which depends on field studies, is generally absent from the literature on salticids, but all salticids, including the myrmicophagic and araneophagic species, appear to be more or less euryphagous (Edwards *et al.*, 1974; Jackson, 1977; Cutler, 1980). The present review, therefore, will concentrate on recent laboratory studies of prey-specific capture behaviour and prey preferences.

Prey-specific capture behaviour

Forster (1977, 1982a) analyzed in detail the visually-mediated hunting sequences prevalent in salticid species. The salticid first orients by swivelling its cephalothorax around to bring the principal (AM) eyes to bear on the prey. Next, it aligns its abdomen with its cephalothorax and begins a pursuit, usually by stalking slowly in an almost cat-like manner, towards the prey. When close, the salticid lowers its body and fastens a dragline to the substrate, pauses, then leaps onto the prey. Although this appears to be the typical predatory sequence for most salticid species, myrmicophagic and araneophagic salticids are exceptions.

Araneophagic salticids

Eating other spiders appears to be an opportunistic occurrence for most spiders, a larger or faster individual overpowering another in a chance encounter, but there are numerous exceptions. Some salticids make a practice of leaping or

walking into webs to catch the resident spider (Tolbert, 1975; Robinson & Valerio, 1977; Jackson, 1985a, b, 1986a, 1988). However, the most extreme specialization on spiders as prey is known in ten species of salticids (from 4 genera), all from the subfamily Spartaeinae (Wanless, 1984). These species practise vibratory aggressive mimicry in other spiders' webs, where they sometimes capture spiders larger than themselves. In the present review, the term 'araneophagic salticids' is restricted to these species (Jackson, 1992a). Each of these species also preys on insects (either in or out of webs), and the Queensland *Portia fimbriata* also preys on other salticids. A large spider (because it is dangerous), another salticid (because it can see well) or a spider in a web (because it is in a special environment - a web) would all seem to be something that a salticid, as a predator, would perceive as special. The most important common factor is probably that these spiders tend to be, for salticids, difficult-to-catch and dangerous potential prey - the potential prey is also a potential predator.

In a web, an araneophagic salticid's strategy is usually not simply to stalk or chase down the resident spider but instead to send vibratory signals across the silk (aggressive mimicry). The resident spider may respond to these signals in a way that appears indistinguishable from how it would respond to a small insect ensnared in the web, but when the duped spider gets close, the araneophagic salticid lunges out and catches it.

The most extensively studied araneophagic salticids are from the genus *Portia*, and in these species aggressive mimicry is combined with pronounced behavioral complexity (Jackson & Pollard, 1996). *Portia* has a large repertoire of vibratory signals (Jackson & Wilcox, 1993a) made by manipulating, plucking and slapping the silk with one or any combination of its legs and palps, all of which can be moved in different ways. *Portia* also makes signals by flicking its abdomen, and abdominal movements can be combined with all of the appendage movements. Many of these behaviours by which *Portia* makes signals appear to be evolutionary modifications of grooming behaviour (Jackson & Hallas, 1990).

The web-building spider, *Portia*'s intended victim, has acute abilities to detect and discriminate between vibratory signals transmitted over the silk in its

web, but how the spider interprets these web-borne vibrations varies considerably between species and also with the sex, age, previous experience and feeding state of the spider (Witt, 1975; Jackson, 1986a; Masters *et al.*, 1986). Yet *Portia* has been observed using aggressive mimicry to catch many kinds of web-building spiders, within a range of about one tenth to twice *Portia*'s size (Jackson & Blest, 1982b; Jackson & Hallas, 1986a). Preliminary results suggest that the key to *Portia*'s success at victimizing so many different types of spiders is an interplay of two basic ploys: 1) using prey-specific (fixed) signals when cues from some of its more common prey species are detected (Jackson & Wilcox, 1990); and 2) using feedback to adjust signals to different prey species (Jackson & Wilcox, 1993a). The first ploy, using fixed tactics, is consistent with the popular potrayal of spiders as animals governed by instinct. With the second ploy, *Portia* solves problems: *Portia* dtermines, by trial and error, what to do with different victims. Other problem-solving abilities include making detours when approaching prey (Jackson & Wilcox, 1993b; Tarsitano & Jackson, 1992, 1994) and somkescreen behaviour (Wilcox *et al.*, 1996).

A number of spider species from several families other than the Salticidae are also web-invading araneophagic spiders that use aggressive mimicry (Jarman & Jackson, 1986; Jackson & Whitehouse, 1986; Whitehouse, 1986; Jackson & Brassington, 1987). However, web-invading araneophagic salticids appear to differ in important ways from the web-invading araneophagic spiders of other families. Araneophagic salticids can walk across both ecribellate and cribellate sticky webs without getting stuck (Jackson, 1986a), and they are highly effective at preying on a wide array of web-building spiders. In contrast, none of the araneophagic non-salticid spiders studied can cross both cribellate and ecribellate sticky webs unimpaired. Also, the set of web-building spiders caught by araneophagic non-salticid spiders is considerably smaller than that of the araneophagic salticids, and the predatory strategies of the araneophagic non-salticid spiders appear to be less complex than those of the araneophagic salticids (Jackson, 1992a). Signal output variation appears important in enabling both salticid and non-salticid aggressive mimics to achieve fine control over the responses of each particular victim spider. However, compared to the

araneophagic non-salticid spiders, the araneophagic salticids use a larger repertoire of vibratory signals and they combine and vary their signals more extensively. Unlike the araneophagic non-salticid spiders, the araneophagic salticids have acute vision (Jackson & Blest, 1982b) and are not restricted to interpreting web vibrations when detecting, identifying, and locating prey on webs. The absence of acute vision may have been an important constraint limiting the range of prey taken by the araneophagic non-salticid spiders (Jackson, 1986a, 1992a).

Although not so extensively studied as *Portia*, the other aggressive-mimic salticids (*Brettus*, *Cryba* and *Gelotia*) also readily invade many different types of webs and also resemble *Portia* by using strategies based on a combination of fixed signals and trial-and-error behaviour (Jackson & Hallas, 1986c; Jackson, 1990a, b; Jackson & Wilcox, 1993a). However, the genera of araneophagic salticids differ markedly in the methods used for catching prey. For example, *Brettus*, *Cyrba* and *Gelotia* are generally more inclined than *Portia* to remain near the edge of the web (Jackson & Hallas, 1986c). However, the most well-studied differences are among the species, and even populations of single species of *Portia*.

The most pronounced example of interpopulation difference in predatory behaviour is the Queensland population of *P. fimbriata*, which differs from all other *Portia* studied by having special methods for catching cursorial salticids belonging to other genera. *P. fimbriata*'s habitat in Queensland is unique among those studied in having an abundance of cursorial salticids (Jackson & Hallas, 1986a) and, apparently, the Queensland *P. fimbriata*'s predatory behaviour is specially adapted to this locally abundant type of prey (Jackson, 1992b).

In the open, the Queensland *P. fimbriata* uses cryptic stalking, a special kind of trickery, but not an example of aggressive mimicry (Jackson & Blest, 1982a). The Queensland *P. fimbriata*, in common with all *Portia*, has an unusual (cryptic) appearance; because of markings, tufts of hairs, and long, spindly legs, *Portia* resembles a piece of detritus and a slow, choppy gait probably helps a moving *Portia* preserve detritus resemblance. Crypsis, which probably provides *Portia* with protection against its own visually hunting predators, is also important

in relation to cryptic stalking. When cryptically stalking a salticid, *P. fimbriata* moves especially slowly, pulls its palps back and out of its prey's view, and freezes if the salticid turns to face it, thereby concealing itself from this special type of prey spider which, in common with *Portia*, has acute eyesight. Eventually, the Queensland *P. fimbriata* approaches the salticid from behind, then swoops down to kill it. In addition, the Queensland *P. fimbriata* is unique among *Portia* studied because it makes vibratory signals on the nests of salticids to entice them out and catch them (Jackson & Hallas, 1986a). Furthermore, the Queensland *P. fimbriata* has a special tactic for catching *Euryattus*, a salticid sympatric with the Queensland *P. fimbriata*, but not sympatric with any other *Portia* studied: the Queensland *P. fimbriata* mimics the unique courtship signals of *Euryattus* males to lure *Euryattus* females out of suspended rolled-up leaves and attack them (Jackson & Wilcox, 1990).

Myrmicophagic salticids

Ants come equipped with strong mandibles, poisonous stings and formic acid (Eisner, 1970; Blum, 1981). Also, being social insects, ants tend to be present in large numbers and can mount communal attacks on predators and prey (Wilson, 1971). All of these factors tend to present formidable challenges to most cursorial spiders (Nentwig, 1986). However, in most terrestrial environments, and especially in the tropics (where salticids appear to be the dominant spider family: Bristowe, 1941), ants are the dominant arthropods in the size range of the prey normally taken by salticids (Hölldobler & Wilson, 1990). For a salticid that overcomes the ant's defence, a rich food resource becomes available.

Ants and certain other arthropod groups (*e.g.*, bees, wasps, carnivorous bushcrickets, etc.) present salticids with a problem similar to spiders as prey: they are unusually difficult-to-catch and dangerous, and apparently one of the most effective ways for salticids to exploit ants is with specialized (*i.e.*, prey-specific) capture behaviour. Also, for ants, as for spiders, apparently only a minority of salticid species routinely preys on these heavily defended prey (see Robinson & Valerio, 1977). The capture behaviour of 9 myrmicophagic salticid species (6

belonging to subfamily Heliophaninae and 3 to subfamily Euophrynae) has been studied in detail and each of these 9 species preys not only on ants but also on other (more conventional) prey insects (*e.g.*, flies). Each has evolved prey-specific capture behaviour for use against ants, which differs from the predatory behaviour they use to capture other insects (Edwards *et al.*, 1974; Cutler, 1980; Wing, 1983; Jackson & van Olphen, 1991, 1992; Jackson & Pollard, 1996; Chapter 2).

Predatory behaviour used against ants varies among the species, but the six heliophanines are remarkably similar to each other, while differing from each of the three euophryines. Among the euophryines, *Zendorus* (formerly *Pystira*) *orbiculata* differs considerably in behaviour from another two euophryines, *Corythalia canosa* (Jackson & van Olphen, 1991) and *Habrocestum pulex* (Chapter 2). *C. canosa* and *H. pulex* resemble each other by manoeuvring to attack the ant head on. However, unlike *C. canosa*, *H. pulex* never holds its body raised while pursuing, attacking and starting to feed on ants. *Z. orbiculata* attacks ants from just about any orientation. However, *Z. orbiculata*, unlike the other myrmicophagic salticids, also often positions itself facing down on ant-infested tree trunks and ambushes ants by lunging down on them instead of actively pursuing them. *H. pulex* resembles the heliophanines by often stabbing ants then backing away. However, *H. pulex* usually attacks ants head-on. The heliophanines (Jackson & van Olphen, 1992) sometimes attack ants head on, but they also often attack from directly behind the ant. Not only do all these species stab the ant and attack from directly behind it, but they also usually hold legs I elevated while pursuing, attacking and starting to feed on ants. In contrast, *C. canosa* (Jackson & van Olphen, 1991) tends to hold its cephalothorax, but not its legs I, elevated.

Prey preferences of specialized salticids

We ask three questions about araneophagic and myrmicophagic salticids: 1) Do the species with prey-specific capture behaviour for catching dangerous

prey (*i.e.*, ants and spiders) prefer these dangerous prey? 2) Do these species prefer certain sizes of prey? 3) Do males and females of these species prefer the same prey?

Testing methods

Nentwig (1986) investigated the prey preferences of a wide variety of spiders using different types of prey presented sequentially, and he found evidence of selectivity. A similar method used in an early study of *Portia*'s prey preferences (Jackson & Hallas, 1986a) found that *Portia* preferred spiders to insects as prey. Also, there have been three prey-preference studies of *Phidippus audax*, a common North American salticid: each found evidence of selective predation when different prey were presented simultaneously (Givens, 1978; Freed, 1984; Roach, 1987).

However, the studies we now review differ from the above studies of prey preferences: for each species reviewed here, three distinct types of tests for prey preference were carried out (Jackson & van Olphen, 1991) - 1) one individual of one type of prey presented to a predator at a time on alternate days, sequence decided randomly; 2) two types of prey presented to a predator simultaneously, one individual prey of each type; and 3) feeding predator presented with one individual of an alternative prey type, sequence for alternate days decided randomly. A strength of these testing routines is that, for each salticid species tested, findings from the different test designs can be compared for consistency. Consistent evidence of the same preference across test designs makes conclusions especially convincing.

Taxonomic categories of prey preferred

Each of 9 species of myrmicophagic salticids studied not only uses a prey-specific behaviour for catching ants, and a different prey-specific behaviour for catching other insects, but also has a distinct preference for ants over other varied types of prey as demonstrated by consistent results across Type 1 - 3 tests (Jackson & Olphen, 1991, 1992; Chapter 2).

All of the araneophagic salticids that are known to have prey-specific

behaviour for catching spiders (*i.e.*, *Brettus*, *Cyrba*, *Gelotia* & *Portia*) also appear to prefer spiders to insects as prey (Jackson, 1992a). However, information from detailed studies based on Type 1 - 3 tests is available only for *Portia fimbriata* from Queensland (Chapter 4) and *Portia labiata* from Sri Lanka (Chapter 5). These studies show that *P. fimbriata* and *P. labiata* are behaviourally specialized as predators on web-building spiders in two distinct ways: besides using prey-specific capture behaviour against web-building spiders (Jackson, 1992a), consistent results from Type 1 - 3 tests show that they also have pronounced preferences for web-building spiders to insects (Chapter 4 & 5).

Queensland *P. fimbriata* is of special interest because of the unusual component of this *Portia*'s diet: they frequently eat other species of salticids in nature (Jackson & Blest, 1982a). Remarkably, not only does the Queensland *P. fimbriata* use specialized prey-catching behaviour against the salticids on which it preys, but also, from consistent results across Type 1 - 3 tests show that they prefer salticids to other spiders as prey (Chapter 4). The Queensland *P. fimbriata* appears to have a hierarchy of prey preferences: on a broader scale, it prefers spiders (both cursorial salticids and web-building spiders) over insects; on a finer scale, it prefers cursorial salticids over web-building spiders.

Portia labiata and the Queensland *P. fimbriata* are behaviourally different because there is no evidence that *P. labiata* uses cryptic stalking or any other prey-specific capture behaviour against cursorial salticids and, in contrast to the Queensland *P. fimbriata*, *P. labiata* is decidedly ineffective at catching cursorial salticids (Jackson & Hallas, 1986a, b). The contrast between *P. labiata* and Queensland *P. fimbriata* extends also to prey preferences: results from Type 1 - 3 tests showed that *P. labiata* prefers web-building spiders to cursorial salticids (Chapter 5). Evidently, local abundance of cursorial salticids has also shaped the evolution of, not only salticid-specific capture behaviour, but also prey preferences.

The biology of the myrmicophagic and araneophagic salticids studied suggests that, when predators evolve prey-specific capture behaviour for use against dangerous prey, they also tend to evolve distinct preferences for these dangerous prey. Why this might be so is not obvious. Detailed comparative

studies of non-salticid predators are needed to clarify how broadly applicable this trend is in animals.

Males and females compared

In nature, males of all species of *Portia* studied resemble females by frequently feeding on web-building spiders (Jackson & Blest, 1982a; Jackson, unpubl. data). Also, males of all species of *Portia* studied use the same prey-specific prey-catching behaviours against web-building spiders as females (Jackson & Blest, 1982a; Jackson & Hallas, 1986a). In the laboratory, an additional similarity has been illustrated: in Type 1 - 3 tests, both the males and the females of the Queensland *P. fimbriata* (Chapter 4) and the Sri Lanka *P. labiata* (Chapter 5) took web-building spiders in preference to insects as prey.

Furthermore, males of the Queensland *P. fimbriata*, in common with females, frequently prey on cursorial salticids (Jackson & Blest, 1982a; Jackson, unpubl. data) and both males and females also use cryptic stalking against cursorial salticids (Jackson & Hallas, 1986a). Also, in Type 1 - 3 tests, both males and females of the Queensland *P. fimbriata* take cursorial salticids in preference to web-building spiders as prey (Chapter 4). In contrast, in Type 1 - 3 tests, both males and females of the Sri Lanka *P. labiata* take web-building spiders in preference to cursorial salticids as prey (Chapter 5).

Females of spiders appear to have evolved a lifestyle that emphasizes the consumption of large quantities of food as an adaptation for adding yolk to eggs. Males, in contrast, appear to have evolved a lifestyle emphasizing courtship, mating, and searching for females (see Vollrath & Parker, 1992). Because male lifespan is generally short and food requirements are smaller than for females, a preference by males for prey smaller than that preferred by females might be expected. Evidence of this difference was first demonstrated for *Phidippus audax*, a common North American and predominantly insectivorous salticid: *P. audax* males tend to take smaller prey than females (Givens, 1978). A similar interspecific difference was found in the Queensland *P. fimbriata*: in Type 1 - 3 tests, males Queensland *P. fimbriata* took smaller spiders (both web-building spiders and cursorial salticids) than did females (Chapter 4).

Effect of hunger on prey preference

Although hunger has numerous influences on the behaviour of predators (Curio, 1976), including salticids (Drees, 1952; Gardner, 1964), little is known about how hunger affects the prey-preference behaviour of salticids. Recently, hunger was investigated in araneophagic and myrmicophagic salticids and found to vary among the species studied. In *Corythalia canosa*, *Chrysilla lauta*, *Natta* spp. and *Siler semiglaucus* (Jackson & van Olphen, 1991, 1992), well-fed individuals had distinct preferences for ants, but these preferences broke down when these myrmicophagic salticids had been starved for two weeks before testing. When starved, these ant-eating species took ants and other insects indiscriminately. However, prey preferences of myrmicophagic *Habrocestum pulex* (Chapter 2), and araneophagic *P. fimbriata* (Chapter 4) and other *Portia* (Chapter 5) were not affected by a 2-week period without food. Why hunger influences these species differently is currently unclear.

The role of vision in prey preference

The distinguishing characteristic of salticid spiders is their complex eyes (Land, 1974; Forster, 1982a, b; Blest & Carter, 1987; Blest *et al.*, 1990). The principal eyes are responsible for acute vision (Homann, 1928; Land, 1969a, b, 1971), allowing the salticid to identify mates, rivals and predators from distances of 30 body lengths or more (Jackson & Blest, 1982b; Jackson, unpubl. data). Exceptionally good eyesight has probably facilitated the evolution of pronounced preference behaviour in these spiders: evidently, these salticids can discriminate, prior to contact, between different types of prey (Jackson & Blest, 1982b).

The cues used by typical salticids for distinguishing between insect prey and other objects such as mates, rivals, enemies and irrelevant stimuli, have been investigated extensively. Shape, symmetry, presence of legs and wings, size, and style of motion (short, jerky movements) are some of the more important features by which these salticids appear to recognize their prey (Heil, 1936; Crane, 1949, Drees, 1952; Forster, 1979, 1982a, b; Edwards, 1980).

However, for salticids with predatory versatility and pronounced prey preferences, we have little information about the cues that influence the various components of the complex predatory strategies.

Most of what we know concerns the cues that govern *Portia*'s decisions of whether to enter a web, whether to make signals once in a web, and whether to persist at signalling once started. Seeing a web elicits web entry, but volatile chemical cues from webs of prey spiders do not appear to be important. Seeing a spider in a web increases *Portia*'s inclination to enter the web. After web entry, cues from the web are sufficient to elicit signalling behaviour, even in the absence of other cues coming directly from the prey spider. Seeing a prey spider or detecting vibrations on the web make *Portia* more prone to signal, but volatile chemical cues from the prey spiders themselves do not appear to be important. Once *Portia* is on a web and signalling, seeing a moving spider and detecting vibrations on the web encourage *Portia* to persist in signalling (Jackson, 1995).

Prey movement is an especially effective stimulus for eliciting orientation and pursuit by typical salticids (Drees, 1952; Dill, 1975). Different patterns of movement may also permit salticids to distinguish between different types of prey (Freed, 1984). However, movement is not always necessary. Anecdotal evidence suggests that typical insectivorous species of salticids occasionally stalk and attack motionless prey (see Forster, 1985), and *Portia* preys readily on quiescent web-building spiders in nature and in the laboratory (Jackson & Hallas, 1986a). Additionally, in the laboratory *Portia* can distinguish between quiescent spiders, insects and eggsacs using visual cues alone (Jackson, 1995). Also, eleven salticid species, including *Corythalia canosa* (a myrmicophagic salticid) and four species of *Portia* (araneophagic salticids), stalk and attack completely motionless (dead) prey. The myrmicophagic and araneophagic salticids used the same prey-specific capture behaviour with the different kinds of motionless prey that they normally used with the same kinds of living prey (Jackson & Tarsitano, 1993). Also, the prey preferences of two species of araneophagic salticids, the Queensland *P. fimbriata* (Chapter 4) and other *Portia* (Chapter 5), and one species of myrmicophagic salticid, *Habrocestum pulex* (Chapter 2), have been investigated in tests using dead, motionless prey and shown to be the same as

in tests using living prey. These studies suggest that cues from prey shape alone are sufficient to elicit prey-specific capture behaviour and prey preferences in salticids.

Drees (1952), in an experimental study using *Evarcha plancardi*, used lures to investigate the cues by which this insectivorous salticid distinguishes between prey (insects, to be attacked) and other salticids (mates or rivals, to be displayed at). He found that an effective model for evoking conspecific displays had to have a central 'body' and a series of 'legs' on each side, with the legs making appreciable angles. More legs made lures more effective at eliciting displays. In contrast, lures taking a wide variety of forms were effective at eliciting attacks as long as they moved and were not appreciably larger than the salticid. Drees' (1952) experiments suggest that the insectivorous salticid's rule is: "if it moves, find out whether it has legs in the right places; if it does, display; if it does not, try to catch it". However, for myrmicophagic and, especially, araneophagic salticids, the rules must be considerably more complex. The Queensland *P. fimbriata* is perhaps the most complex, as it preys not only on other spiders but also on other species of salticids. The cues by which myrmicophagic and araneophagic salticids distinguish between different types of prey are currently being investigated.

Questions about the cues used by salticids with predatory versatility highlight how far we remain from fully understanding the functioning of the salticid visual system. Although salticid eyes are large and complex for a spider, this is no primate (Land, 1974). The principal eye lens is only a few millimetres in diameter, and there are only a limited number of receptors in the salticid eye and neurons in the salticid brain. How so small a visual system, with so few components, is able to perform these perceptual feats is currently a mystery.

CHAPTER 11

Discussion

Preface

This is a more complete discussion than in Chapter 10. For example, additional work, not completed when the conference paper (Chapter 10) was prepared for the XIII International Congress of Arachnology (Geneva, Switzerland, September 1995), can now be reviewed. Also, the conference paper did not allow space for the synthesis that will be attempted in this chapter (Chapter 11).

Behavioural specialization

In Chapter 10, predatory versatility was defined as when a predator has a conditional strategy: different prey-specific capture behaviour is used against different prey. A predator that uses a prey-specific capture behaviour can be called 'specialized in behaviour'. However, another way in which a predator may be specialized is to prefer particular prey and this is distinct from a predator's prey-specific capture behaviour. Consequently, the term 'specialized predator' is not very precise since it might mean a predator that has either prey-specific capture behaviour, a preference for a particular type of prey or both. In my thesis, I attempted to clarify this distinction by investigating the interrelationship of predatory versatility and prey preference in salticid spiders.

Salticids are of special interest because this group has evolved unique, complex eyes and highly acute vision (Land, 1969a, b; Jackson & Pollard, 1996). Having acute vision, pronounced prey preferences might be especially likely to evolve in these spiders.

Araneophagic salticids

Spiders that prey routinely on other spiders (*i.e.*, practise araneophagy) are known from several families, including Mimetidae, Theridiidae, Pholcidae, Lamponidae, Gnaphosidae, and Salticidae (Jackson, 1992a). In the Salticidae, araneophagy is known in ten species (from 4 genera): five species of *Portia* (*P. africana* and *P. schultzi* from Kenya; *P. albimana* from Sri Lanka; *P. labiata* from Malaysia and Sri Lanka; *P. fimbriata* from Australia, Malaysia, and Sri Lanka), two species of *Brettus* (*B. adonis* and *B. cingulatus* from Sri Lanka), one species of *Gelotia* (*G. lanka* from Sri Lanka), and two species of *Cyrba* (*C. algerina* from southern Europe and *C. ocellata* from Australia, Kenya, Sri Lanka, and Thailand), all from the subfamily Spartaeinae (Wanless, 1984). Predatory versatility is pronounced in each of these 10 species. Each preys not only on spiders but also on insects, and each hunts both in or out of webs. Each is a behaviourally specialized predator that uses different prey-specific capture behaviours against different types of prey. However, the prey preferences of these salticids are poorly understood.

The most extensively studied araneophagic salticids are from the genus *Portia* (Jackson & Pollard, 1996) and, in particular, the species *P. fimbriata* from Queensland. There are at least 15 species (Wanless, 1978, 1984; Peng *et al.*, 1993) in this genus of African, Asian, and Australian salticids initially thought to be tropical in distribution. However, *Portia quei* (Zabka, 1985) and *Portia heteroidea* are recently described species from subtropical China (Xie & Yin, 1991).

Five species of *Portia* (*P. africana* and *P. schultzi* from Kenya; *P. albimana* from Sri Lanka; *P. labiata* from Malaysia and Sri Lanka; *P. fimbriata* from Australia, Malaysia, and Sri Lanka) have been subjects of earlier behaviour studies, and each of these species of *Portia* uses prey-specific capture behaviour against a wide range of web-building spiders. Also, in each species, males and females appear to have similar predatory strategies (Jackson & Hallas, 1986a).

Also, there appears to be a strong trend in *Portia* with regard to preferences. In my thesis, I studied four species of *Portia* (*Portia fimbriata* from Queensland, *P. africana* and *P. schultzi* from Kenya and *P. labiata* from Sri Lanka

and the Philippines) and found that each of these species has a distinct preference for web-building spiders to insects as prey, and both the males and the female of these species also have pronounced preferences for web-building spiders over insects. Although further comparative study is needed, these findings suggest that preference for web-building spiders over insects may be general in the genus of *Portia* and, perhaps other araneophagic spartaeine genera (*Brettus*, *Cyrba*, and *Gelotia*).

However, in *Portia*, details of behaviour vary among species and even among populations of single species. In particular, it appears that, uniquely in the habitat in which *P. fimbriata* lives in Queensland, cursorial salticids are extremely abundant (Jackson & Hallas, 1986a; Jackson, 1988), and the Queensland *P. fimbriata* has a prey-specific capture behaviour for use against this locally abundant type of prey (Jackson, 1992b).

There appears to be an interesting parallel in how prey preference and prey-specific capture behaviour differ among the species of *Portia* studied. The Queensland *P. fimbriata*, but not the other *Portia* studied, uses a salticid-specific capture behaviour (Jackson & Hallas, 1986a), and also the Queensland *P. fimbriata* prefers salticids to web-building spiders. However, *P. africana*, *P. labiata* and *P. schultzi* consistently take web-building spiders in preference to salticids. It appears that local abundance of cursorial salticids has shaped the evolution of, not only salticid-specific capture behaviour, but also prey-preference behaviour in Queensland *P. fimbriata*.

The Queensland *P. fimbriata* prefers salticids to flies. Preference for salticids over flies does not appear to be so strongly expressed in *P. africana*, *P. labiata* and *P. schultzi*; males and females of each of these species attacked salticids more often than they attacked flies in Type 1 and 2 tests, but there was no evidence of preference in Type 3 tests. Type 3 tests, where the criterion for preference comes from the predator dropping one prey to take another, might be envisaged as a test for stronger preference than Type 1 and 2 tests.

Myrmicophagic salticids

Araneophagic salticids have evolved to be specialized predators on

dangerous prey (*i.e.*, spiders) that are abundant in the same habitat with the predator. This raises the question of whether other salticids might have evolved to be specialists on other types of common but dangerous prey. Other prey that might fit this description, and which fall in the correct size range for a salticid, include wasps, bees, predatory bush crickets and ants. Ants are perhaps the most interesting, as most salticids appear to avoid close proximity with ants (Bristowe, 1941). Widespread ant-avoidance behaviour is understandable as ants are frequent predators of salticids. Also, ants are social insects that tend to be present in large numbers (Hölldolber & Wilson, 1991), which may make them, not only especially dangerous, but also potentially a bonanza for a salticid that can overcome the ant's defences. A salticid able to prey on this dangerous and abundant type of prey has access to a rich food source not available to competitors that can not take this prey (see Nentwig, 1986).

Ants have potent chemical and mechanical defences which appear to be sufficient to repel attacks by most salticids. These defences include formic acid, stings and strong mandibles (Evans, 1984). However, there is an interesting minority of salticids that routinely feeds on ants, and these species are known to be behavioural ant specialists (Edwards *et al.*, 1974; Robinson & Valerio, 1977; Cutler, 1980; Jackson & van Olphen, 1991, 1992; Chapter 2 & 3), although the diet of none of these salticids is restricted solely to ants. Instead, the ant specialists also readily attack other more typical salticid prey (*e.g.*, flies). These species are behavioural ant specialists in that they have evolved specialized (prey-specific) capture behaviours that enable them to overcome the ant's defences.

Ant-eating specialization has been most thoroughly studied in 14 salticid species, each of which lives in habitats in which ants are abundant. The first salticid demonstrated to be specialized at eating ants was *Corythalia canosa* (formerly *Stoidis aurata*)(Edwards *et al.*, 1974). Subsequently, comparative data have become available for another 13 species of myrmicophagic salticids: *Habrocestum pulex* from North America (Cutler, 1980; Chapter 2), *Zendora* (formerly *Psytira*) *orbiculata* from Queensland, 4 species of *Natta* sp. from Kenya, *Chrysilla lauta* and *Siler semiglaucus* from Sri Lanka (Jackson & van Olphen,

1991, 1992), *Siler* sp., *Chalcotropis* sp., *Telamonia masinloc*, and two new species of euophryines in a new genus (referred to herein as *Euophrys* sp. 1 and 2)(Chapter 3). Thirteen of these myrmicophagic salticids appear to have evolved specialized capture behaviour for use against ants that is distinct from the behaviour that these same salticids use to capture other insect prey. *Telamonia masinloc* is the exception. However, all 14 species, including *Telamonia masinloc*, appear to have evolved pronounced preference for ants over other insect as prey.

There appears to be an interesting taxonomic bias in the distribution of myrmicophagic salticids: all but one of the species of myrmicophagic salticids known are in one or the other of two subfamilies, Euophryinae (*Chalcotropis* sp., *Corythalia canosa*, *Euophrys* sp. 1 and 2, *Habrocestum pulex*, *Zendora orbiculata*) or Heliophaninae (*Chrysilla lauta*, *Siler semiglaucus*, *Siler* sp., and 4 species of *Natta*), *Telamonia masinloc*, a plexippine, is the exception.

The higher-order systematics of salticids is poorly understood, making conclusions about phylogenetic trends difficult to draw. Also, little is known about the predatory behaviour of other euophryine and heliophanine salticids. However, these findings suggest that myrmicophagy has evolved especially in these two subfamilies. *Euophrys parvula* from New Zealand is nominally a euophryine and this species is not myrmicophagic (Depree, 1992). However, New Zealand salticid taxonomy is very poorly studied, and *E. parvula* is probably not a true euophryine. Therefore, information available does not clearly contradict the hypothesis that it is especially in euophryine and heliophanine salticids that myrmicophagy has evolved. However, in plexippines, myrmicophagy appears clearly not to be a subfamily-wide character. Besides *Telamonia masinloc* *Plexippus paykulli* is the only plexippine species for which predatory behaviour has been studied in detail, and there is no evidence that this species is myrmicophagic (Jackson & Macnab, 1989).

Specialized predation by Philippines Portia labiata on Scytodes

Scytodes sp. indet. is an abundant and especially interesting prey of Philippines *Portia labiata* in Los Banos. *Scytodes* (Scytodidae) is a genus of tropical and subtropical spiders with unusual predatory and anti-predatory

behaviours: these species spit a sticky gum from their chelicerae over prey (Monterosso, 1927; Bristowe, 1958; Dabelow, 1958) and predators (McAlister, 1960; Gilbert & Rayor, 1983). In the Philippines, *Scytodes* sp. indet. uses spitting behaviour routinely to prey on salticid spiders (Chapter 6). Yet *Portia labiata*, a salticid, routinely preys on *Scytodes*.

In nature, the Philippines *Scytodes* lives primarily on leaves of trees, where it builds a small web. Salticids are common in the same habitat, foraging on the same leaves. *Scytodes*, in common with most web-building spiders, has poor vision. Its ability to detect a salticid appears to be based primarily on interpreting the signals, either silk-bourn or leaf-bourn, made by the salticid as it moves about in the environment. If a salticids stumbles across a line of silk, the scytodid rushes out and spits on it. If the salticid runs away, the *Scytodes* may leave its web, chase after the salticid and capture it by spitting. Alternatively, the *Scytodes* may go on hunting forays completely away from the web where it apparently detects the salticid's distinctive stop-and-go walking gait through the leaf alone, without depending on web lines at all (Chapter 6).

In the Philippines, *P. labiata* lives in this same habitat, hunts on the same leaves, and frequently preys on *Scytodes* by entering *Scytodes*' web and luring the spider out, carefully avoiding provoking a spitting attack from *Scytodes* (Chapter 7), This is important because sometimes the tables are turned and *Portia* becomes its intended meal's meal.

Four species of web-invading salticids (and, for *Portia labiata*, two populations) were tested with *Scytodes* in the laboratory: *Portia fimbriata* and *Jacksonoides queenslandica* from Queensland; *P. labiata* from Sri Lanka; *P. labiata* and *Ligurra* sp. from Los Banos in the Philippines. Three of these four species were observed to capture *Scytodes*: *P. fimbriata*, *P. labiata*, and *Ligurra*. *Ligurra* always leapt into webs, but *Portia fimbriata* and *P. labiata* walked slowly into webs and practised aggressive mimicry.

The two species of *Portia* consistently used aggressive mimicry and they were also more efficient than *Ligurra* at catching *Scytodes*, suggesting that aggressive mimicry is critically important as a tactic by which *Portia* circumvents the defence of *Scytodes*. However, fine tuning of how aggressive mimicry is used

appears to be important as well. Even though *P. fimbriata* (Q) used aggressive mimicry, it was more likely to elicit spitting and less efficient at catching *Scytodes* than *P. labiata* (LB). *P. fimbriata* (Q) appeared to make inappropriate aggressive mimicry signals for this particularly dangerous prey spider (*i.e.*, vibrating the web by fluttering alone or by a combination of fluttering and striking). In contrast, *P. labiata* (LB) was more likely to signal by plucking on the web with its palps. The use by *P. labiata* (LB) of appropriate signals against *Scytodes* appears to be an instance of local adaptation to a locally abundant prey: *P. labiata* (LB) apparently has evolved *Scytodes*-specific pre-programmed tactics for precisely controlling the behaviour of the *Scytodes* on which it preys.

Detouring is also important for understanding why *P. labiata* (LB) is successful at catching *Scytodes*: *P. labiata* (LB) was more likely than *P. fimbriata* (Q) and *P. labiata* (SL) to make a detour to a better vantage point before leaping onto *Scytodes*. *P. labiata* (LB)'s signal-detour-leap sequence appears to be an especially effective tactic for overcoming the special defence of *Scytodes* and for catching this unusually dangerous spider.

What factors account for this fine tuning of the complex predatory strategy of *P. labiata* (LB)? The abundance of *Scytodes* seems important. Although species of *Scytodes* are also present in Queensland where *P. fimbriata* lives and in Sri Lanka where *P. labiata* lives, *Scytodes* is an especially abundant prey spider in Los Banos and sympatric with *P. labiata* (LB). It would appear that a selection regime, from the combination of *Scytodes* being both abundant and exceptionally dangerous, has been responsible for *P. labiata* (LB) evolving prey-specific capture behaviour for this particular prey in its diet. Perhaps this is not surprising. However, *P. labiata* (LB)'s preferences appears also to have been influenced by this selection regime, and why this might be so is less obvious.

The Philippines *P. labiata* (LB) not only has prey-specific capture behaviour for *Scytodes*; it also distinguishes between brooding and non-brooding *Scytodes* and prefers the former (Chapter 8). *Scytodes*'s spit comes out of the chelicerae, but a brooding *Scytodes* female carrying eggs tends to be temporarily disarmed, and therefore less dangerous for a *Portia*. *P. labiata* (LB)'s preference for brooding *Scytodes* over non-brooding *Scytodes* as prey appears to be an

example of something that is perhaps common in predators that take especially dangerous prey, but has not often been investigated. That is, these predators may tend to evolve fine tuning of prey preference behaviour, where the fine tuning is related to relative safety: it may be common in these predators that prey preference behaviour has evolved that enables fine distinctions between subclasses of dangerous prey, where the selective advantage of this ability is that it enables the predator to reduce the danger to which it is subjected.

Additionally, predation on spiders may frequently bring araneophagic predators into proximity with the eggs of its prey, and this may well be a food of high nutritive value (Jackson & Blest, 1982a; Jackson & Hallas, 1986a). It is interesting that the Philippines *Portia labiata* (LB) usually first killed the brooding *Scytodes* female, but then released her to pick up and eat the eggs; after feeding on the eggs, *P. labiata* (LB) usually returned to the *Scytodes* female's corpse (Chapter 7).

Questions raised by biology of araneophagic and myrmicophagic salticids

The findings from studies of myrmicophagic salticids (Jackson & van Olphen, 1991, 1992; Chapter 2 & 3) and araneophagic salticids (*P. fimbriata* from Queensland (Chapter 4), *P. labiata* from Sri Lanka, *P. africana* and *P. schultzi* from Kenya (Chapter 5), and *P. labiata* from Los Banos (Chapter 7 & 8)) suggest a hypothesis: when predators evolve prey-specific prey-capture behaviour for use against unusual and dangerous prey, normally unavailable for other related predators, they are also prone to evolve distinctive preferences for these prey. That is, there is a trend for these two different types of behavioural specialization to occur together in the same predator. Why this might be so has rarely been addressed.

Furthermore, this hypothesis may apply within a hierarchy of behavioural specialization. On a broader scale, Queensland *Portia fimbriata* uses specialized prey-catching behaviour against an unusual category of prey (*i.e.*, spiders) and has evolved the behaviour of preferring spiders (both salticids and web-building spiders) to insects as prey; on a finer scale, Queensland *P. fimbriata* has evolved

not only prey-specific prey-catching behaviour for use against salticids but also the behaviour of preferring salticids to other spiders as prey.

Another hypothesis is suggested by the study of Philippines *Portia labiata*'s interactions with *Scytodes*: predators that take especially dangerous prey tend to evolve fine tuning of prey preference behaviour, where the fine tuning is related to relative safety. That is, these predators have tended to evolve prey preference behaviour that enables them to make fine distinctions between subclasses of their dangerous prey, where the ability to make fine distinctions enables the predator to reduce the danger to which it is subjected.

However, a problem arises when we try to define what a "prey type" is in relation to a predator's diet and prey preference (see Drummond, 1983). Is it a particular species, genus, family, order or some other phylogenetic taxa, or is it a size-class or some other non-phylogenetic category, or perhaps a combination of phylogenetic and non-phylogenetic categories? There is probably no easy answer.

When considering araneophagic salticids, order (Insecta or Araneae) was sometimes important. Also, family (Salticidae) and genus (*Scytodes*) was relevant. However, behavioural group (web-building spiders or cursorial spiders) was also important, and these behavioural groups of spiders are not phylogenetic taxa. Also, size-class of prey was sometimes relevant. Whether *Scytodes* was brooding or not seemed to define yet other categories for *P. labiata* (LB). Evidently, researchers interested in preferences must be prepared for the challenge of trying to recognize the classification of prey types that the predators also recognize.

Adaptive trade-offs in salticids: is the jack-of-all-trades the master of none?

Specialization is the ability to perform one or a few activities well. The evolution of specialization has long been of interest to biologists (*e.g.*, MacArthur & Levins, 1964, 1967; MacArthur & Pianka, 1966; MacArthur, 1972; Grant, 1972, 1975; Lawlor & Maynard Smith, 1976; Rosenzweig, 1991; Wilson & Yoshimura,

1994), and tends to be discussed in the context of adaptive trade-offs. That is, there is an expectation that specialization is often at the expense of having to perform other activities poorly. Yet questions about when and if trade-offs become important remain to a large extent unresolved.

Specialization can be considered in relation to a predator's diet or in relation to its behaviour, and care must be taken to remember that diet and behaviour are different things. For a predator, diet is simply what is eaten in nature, and this is determined by not only behaviour but also by what prey are available. It is with respect to behaviour, along with morphology and physiology, that questions about adaptive trade-offs become relative.

The most clear-cut examples of adaptive trade-offs may be from morphology (Curio, 1976). For example, beak shape in birds influences food selection. Seed-eating and nectar-eating birds have beaks of different shapes. Seed eating birds can not get nectar out of flowers, while nectar-eating birds can not crack seeds. Both are specialized and their respective morphological specializations effectively limit them to seeds or nectar. However, some birds have generalized, instead of specialized, beaks, and these generalists are less effective than the specialists at getting seeds and nectar, respectively (Grant, 1986). This suggests that generalists may have an advantage over specialists in exploiting more types of resources, whereas specialists tend to be more efficient than generalists at using their special resource. These ideas about adaptive trade-offs are sometimes referred to as the 'jack-of-all-trades hypothesis' (Curio, 1976; Drummond, 1983): the "jack-of-all-trades is said to be master of none".

The 'jack-of-all-trades hypothesis' is also readily applied to thermal physiology and it is expected that an individual that performs well in its optimal temperature zone ('thermal specialist') should perform more poorly at non-optimal temperature and that a 'thermal generalist' will perform more or less well in a broad range of temperature but not as well as the generalist at the specialist's optimal temperature. However, an alternative pattern of thermal sensitivity can be imagined: a thermal generalist might be imagined with ability to perform better than a thermal specialist at a wide range of temperatures, including the specialist's optimal temperature; logically, we should consider the possibility that

the 'jack-of-all-trades is a master of all' (see Mitter & Futuyma, 1983). That this alternative is not far fetched is illustrated by comparative studies.

The ecological, behavioural, and physiological consequences of thermal sensitivity are important (Hertz *et al.*, 1982; Huey, 1982) because, in ectotherms, body temperature influences that performance of many important physiologically-based systems such as locomotion, digestion, and growth (Brett, 1971; Huey & Stevenson, 1979; Huey, 1982). Huey & Hertz (1984) tested the 'jack-of-all-trades hypothesis' by comparing of the thermal sensitivity of locomotory performance, which should correlate with the animal's fitness (see Arnold, 1983), among five populations of lizards (4 of *Stellio* and one of *Agama savigniyi*). They also compared multiplication rates among protozoans (*Amoeba*). Perhaps unexpectedly, in this study, no evidence of adaptive trade-offs was found: instead of concluding that 'the jack-of-all-trades is the master of none', it appears that in lizards and *Amoeba* 'a jack-of-all-trades is a master of all'. The rank orders of relative running performance were highly correlated across temperature for all four populations of *Stellio* and for *Agama savigniyi* and, thus lizards that ran quickly at one temperature tended to run quickly at all temperatures. Also, rank order of multiplication rates for *Amoeba* at different temperatures remained correlated across temperature intervals. Perhaps adaptive trade-offs do come into play at some unknown level or in some unknown way not revealed by these studies. However, what is perhaps most important about these studies is that they illustrate a need for caution - they remind us that the notion of adaptive trade-offs should not be accepted as a simple truism in relation to thermal biology.

It may be that the 'jack-of-all-trades hypothesis' is problematic in general, not simply in relation to thermal biology. For example, Fox & Morrow (1981), on theoretical and empirical grounds, questioned the hypothesis that physiological specialization leads to increased efficiency in herbivorous insects. How, if at all, the 'jack-of-all-trades hypothesis' applies to the capture behaviour of predators has only rarely been considered. Drummond (1983) compared capture efficiencies of specialist and generalist garter snakes in the laboratory, and his study seems to support the hypothesis: in the laboratory pool, the specialist,

Nerodia sipedon (a water snake), captured significantly more fish and did so faster than two generalists, *Thamnophis sirtalis* and *T. elegans* (garter snakes). Specialized predatory behaviour *N. sipedon* used against fish appeared to be a key factor explaining this species' greater efficiency at catching fish.

In salticids, however, predatory versatility provides examples where adaptive trade-offs are not so obvious. A versatile euryphagous predator, instead of using generalized capture behaviour against all prey types, has a repertoire of prey-specific capture behaviours (Curio, 1976). The versatile predator is, therefore, behaviourally a specialist on multiple prey-types. Applied to groups where predatory versatility has evolved, the jack-of-all-trades hypothesis suggests that the more stenophagous predator, using one (or perhaps a few) discrete prey-specific capture behaviour(s), will be more effective as a predator of the single (or few) type(s) of prey on which it specializes than would be a versatile predator that specializes on this (these) plus additional prey.

How adaptive trade-offs apply to the myrmicophagic salticids studied is not clear. Apparently, during these species' evolution, acquisition of specialized behaviour for taking a difficult type of prey has not necessitated giving up the ability to take 'standard' salticid prey such as flies. Nor does it appear, on the basis of a qualitative comparison, that the myrmicophagic salticids have become less efficient than typical salticids at catching 'standard' prey (Jackson & van Olphen, 1991, 1992; Chapter 2 & 3), although quantitative comparisons of the capture efficiencies of the myrmicophagic salticids during sequences with different types of prey would be valuable.

However, capture efficiencies have been examined quantitatively for *Portia* (Jackson & Hallas, 1986b). Although *Portia* feeds on both spiders and 'standard' salticid prey (fast-moving insects such as flies), *Portia* is not very effective at catching the latter. The reason for this appears to be related to *Portia*'s slow locomotory gait and reluctance to leap on prey. Perhaps decreased effectiveness at catching 'standard' salticid prey came about as an adaptive trade-off in the evolution of crypsis in relation to protection from *Portia*'s own visually-hunting predators, and not so directly as a trade-off brought about by the evolution of araneophagy. However, araneophagy may be indirectly related to hypothetical

trade-offs and the jack-of-all-trades hypothesis: the capture behaviour *Portia* uses against spiders would seem to entail minimal sacrifice of *Portia*'s crypsis in relation to concealment, whereas to adopt the capture behaviour used by typical salticids for feeding on fast-moving prey would entail faster movement and would appear to be detrimental to crypsis (Jackson & Blest, 1982a).

Perhaps more interestingly, there is interspecific and, within *P. fimbriata*, interpopulation variation in apparent size of *Portia*'s repertoire of prey-capture behaviour (Jackson & Hallas, 1986a). This allows me to consider a specific hypothesis about trade-offs. 'Cryptic stalking', a specialized manner of stalking and capturing other salticids, is unique to the Queensland *P. fimbriata*. Otherwise, all species and populations of *Portia* studied use qualitatively the same repertoire of basic categories of predatory behaviour (aggressive mimicry to catch spiders in webs, *etc*). The Queensland *P. fimbriata*, having the prey-specific behaviours ('trades') of the other *Portia* plus one more, can be envisaged as more of a jack-of-all-trades. If there have been trade-offs in the evolution of larger repertoires, then I expect the Queensland *P. fimbriata* to be less effective than other *Portia* at using the shared prey-specific capture behaviour for catching web-building spiders. However, in a quantitative study (Jackson & Hallas, 1986b), the Queensland *P. fimbriata* was found to be more, instead of less, effective as a predator of web-building spiders, counter to the prediction from the hypothesis about trade offs (Jackson & Hallas, 1986b).

It would appear that the hypothesis about adaptive trade-offs should be applied to versatile predators with considerable care. During evolution, versatile salticids appear to have added prey-specific capture behaviours to their predatory repertoires at little or no direct cost.

Traditionally, empirical studies of specialization have tended to focus on comparison between different species, but interspecific comparisons have recently been criticized because traits interpreted to be trade-offs might have arisen after ecological specialization has evolved (Futuyma & Moreno, 1988). That is, many of properties (morphological, physiological and behavioural) of specialized species may be consequences, rather than the causes, of specialization. Also, many different factors may be responsible for a regime of

natural selection favouring the evolution of specialization, whether it be specialization in behaviour, physiology or something else. No one selection factor can be assumed, *a priori*, to explain any individual instance of specialization.

The most useful level at which to study adaptive trade-offs is probably intraspecific variation. The study of *Portia* (Jackson & Hallas, 1986b) is one of the few that has included intraspecific comparison (Queensland versus Northern Territory *P. fimbriata* from Australia), and this did not provide evidence of adaptive trade-offs in the evolution of specialized capture behaviour. The book should probably not be considered closed on the question of whether trade-offs become important when repertoires of capture behaviour get larger, but clearly the notion of adaptive trade offs should not be accepted as a truism.

Optimal diet theory and prey preference

When foraging for prey, it seems logical that a predator should behave in a manner that maximises how efficiently it acquires prey. Things likely to be important for an efficiently foraging predator include ability to assess, recognize, catch and eat prey while minimizing risk, effort and time. These expectations are, to a large extent, the framework for optimal foraging theory (Pyke *et al.*, 1977; Krebs, 1978; Pyke, 1984; Stephens & Krebs, 1986). Optimal foraging theory (OFT) developed following publication of two seminal papers - MacArthur & Pianka (1966) and Emlen (1966). By 1977, what Krebs *et al.* (1983) called 'classical' optimal foraging theory had developed several standard models (Pyke, 1984; Schoener, 1987)

OFT modellers attempt to predict how natural selection has shaped patterns of foraging behaviour, and the utility or 'currency' assumed in classical OFT is usually energy. That is, evolution by natural selection is envisaged as having modified foraging behaviour in one of four basic ways so as to increase the currency (*i.e.*, the net energy intake rate) (Pyke, 1984): 1) diet choice, 2) patch choice, 3) marginal value, and 4) movement. Classical OFT, however, has been extended considerably since 1977 by modifying or even replacing the

assumptions of classical OFT. These extensions have included considerations of central place foraging, risk-sensitive foraging, territory size, foraging mode, and 'rules of thumb' (for reviews, see Pyke *et al.*, 1977; Krebs *et al.*, 1983; Pyke, 1984; Schoener, 1987).

Optimal foraging models provide a way of determining which phenotype, among a set of stated phenotypes, will promote a predator's fitness (*e.g.*, survival, reproductive success, and number of offspring). Popular wisdom, however, has it that arguments against new ideas in science typically pass through three characteristic stages: 'not true' to 'maybe true but not important' to 'true and important, but not new'. It is not surprising that the application of optimal foraging theory to the understanding of animal behaviour currently remains controversial. For some, OFT is anathema - tautological, misguided, and fruitless. For others, it is extremely exciting - programmatic, progressive, and fruitful. Others have less extreme views, seeing OFT basically as a useful tool to be used for as long as it works (Stephens & Krebs, 1986; Schoener, 1987), and this is probably the preferred attitude.

OFT has been criticized for many reasons, some of which have been replied to in detail (Pyke, 1984; Stephens & Krebs, 1986). Some criticisms seem to stem from reading more into the theory than was intended (see Pierce & Ollason, 1987; Gray, 1987). Certainly there are many misunderstandings about OFT. For example, the criticism that OFT ignores constraints misses the point. Constraints can be, should be and are considered when the need for considering them becomes evident. Probably, the most important thing about OFT is that it provides a framework or tool to use in formulating specific hypotheses. No alternative framework is likely to take OFT's place unless it provides a better way to formulate specific hypotheses. Testing and evidence are relevant to the specific hypotheses, not to OFT as a whole. OFT in some global sense is not being tested, nor should it be.

Maximization of net energy intake while minimising net energy expenditure has tended to be the starting point in OFT, and this energy-maximization premise can be said to underpin the whole of current OFT (Krebs *et al.*, 1978; Cheverton *et al.*, 1985; Davey, 1989; Bell, 1991; Krebs & Davies, 1991). This includes

applying OFT to searching for food, exploiting food resources and selecting among alternative food items (Stephens & Krebs, 1986).

Application of OFT to how animals select among alternative food items has been a major subdiscipline and is often called 'optimal diet theory' or ODT (Pyke *et al.*, 1977; Morse, 1980). Araneophagic and myrmicophagic salticids have pronounced preference for spiders and ants as prey, respectively. Does ODT help clarify why these preferences evolved in these species? Clarification of the currency should probably be the first step. We need to know whether spiders or ants, in terms of ODT, are especially profitable prey for these two respective groups of salticids. An index of profitability needs to be clarified for the range of potential prey available to these two types of predators.

Various currencies have been suggested (Cheverton *et al.*, 1985; Stephens & Krebs, 1986) that could affect the prey selected by a predator. That is, a predator's strategy might be to maximize energy intake per unit of time (Schoener, 1971), intake of an essential nutrient (Goss-Custard, 1981; Kennish, 1996), or the nutrient intake needed to ensure adequate nutrition (Westoby, 1978; Greenstone, 1979; Nicotri, 1980; Pierotti & Annett, 1987). Other alternatives might include minimizing risk of starvation, or achieving an optimal balance between risk of predation and the risk of starvation (Krebs & Kacelnik, 1991).

In particular, we need to identify a currency related to the fitness of individuals exploiting a special diet by using prey-specific capture behaviour (see Krebs, 1978; Kamil, 1983). Individuals with specialized predatory behaviour used for a special type of prey and pronounced preference for this prey type might be expected to show correlated benefits in fitness such as survival, lifetime reproductive output, or the number of offspring produced when feeding on this prey. Finding out whether this is so is the logical first step. If it is so, then the second step might be to determine why this diet is favourable to fitness.

Pierotti & Annett (1987) studied the relationship between diet specialization and reproductive output in gulls (*Larus argentatus* and *L. occidentalis*) and found that individual gulls that were specialized on mussels had higher reproductive output (indicated by number of offspring, clutch size, hatching rate, or timing of reproduction) than individual gulls that specialized on other types of food (*e.g.*,

garbage). However, Pierotti & Annett (1987) indicated that the breeding gulls were not behaving simply in a way that met only one of the OFT predictions. Instead, the gulls seemed to base their dietary choices on a number of criteria including factors related to whether they were breeding.

My study on the life cycle of araneophagic *Portia fimbriata* from Queensland indicates that individuals were likely to survive until maturity, mature early, and obtain large body size when reared on spiders (a variety of both web-building spiders and salticids), spiders also being this salticid's preferred prey. However, individuals reared on less preferred prey (a variety of insects) died before reaching the fifth instar (adults usually go through 7-9 instars) and were smaller in size at each developmental stage. When reared on a mixed diet (a variety of spiders and a variety of insects), both body size and survival rate were intermediate (Chapter 9). From this study, it appears that *P. fimbriata* is a predator that prefers the prey that increases its survival rate and other fitness-related consequences. This first step, showing a match up between preference and fitness, has been demonstrated infrequently (see Schoener, 1971; Pyke, 1984). Partly, this may be because the studies needed are labour intensive. For example. in the present thesis, studies of the influence of diet would have been valuable for all species studied, not just *P. fimbriata*. However, the logistics of housing, obtaining prey for, and feeding so many spiders was impracticable within the time span of this Ph.D. thesis.

To forage in a optimal manner, a predator needs ability to discriminate between different types of prey and, by choosing the most profitable type, maximize its fitness (Stephens & Krebs, 1986). That is, predators should rank prey types from most to least profitable and prefer the more to the less profitable prey. In classical OFT, a prey is either absolutely accepted or absolutely rejected by a predator (see references in Pyke *et al.*, 1977). However, recent theory considers how natural selection might shape preferences in more subtle ways. For example, rank-order might depend on both the mean and variance of net energy intake associated with each type of prey ('risk-sensitive foraging theory': Oster & Wilson, 1978; Real, 1980; Caraco *et al.*, 1980; Houston & McNamara, 1985).

A common prediction of ODT models is that predators should accept successively less profitable prey only when higher-ranking prey become scarce (*i.e.*, diet should expand and contract). That is, it is predicted that predators behave so as to be more specialized in diet (*i.e.*, they will be more discriminating) when highly-ranked prey is abundant and they will behave so as to be less specialized in diet (*i.e.*, become more or less indiscriminate in food selection) when highly-ranked prey are scarce.

Hunger is a proximate mechanism by which predators might judge prey abundance. It is predicted that, as predators approach satiation, they will behave as if prey were abundant and become more discriminating (Schoener, 1971; Pulliam, 1974; Charnov, 1976; Glasser, 1982, 1984; Houston & McNamara, 1985). The best evidence for this prediction comes from the work of Ivlev (1961), who showed a significant increase in preference with satiation, and that of Snyderman (1983), who presented pigeons with an operant-conditioning schedule based on the prey choice paradigm and found that the birds became less selective (*i.e.*, took more small items) when tested at high levels of food deprivation.

Well-fed araneophagic and myrmicophagic salticids prefer spiders and ants, respectively, over other prey (*i.e.*, these prey appear to be ranked highest by the respective predators). Based on OFT, we expect increasing hunger to diminish preference (discrimination) in these salticids.

Data on eight of the myrmicophagic salticids studied are consistent with this prediction: in *Corythalia canosa* from America, *Chrysilla lauta* and *Siler semiglaucus* from Sri Lanka, *Zendora orbiculata* from Australia and 4 species of *Natta* from Kenya, well-fed individuals prefer ants to other insects, but individuals of these species, when starved for two weeks prior to testing, appear to take prey indiscriminately (Jackson & van Olphen, 1991, 1992). However, in other myrmicophagic salticids (*Habrocestum pulex* from America (Chapter 2), *Chalcotropis* sp., *Euophrys* sp. 1 and 2, *Siler* sp., and *Telamonia* sp., from the Philippines (Chapter 3)) and in all araneophagic salticids studied (*P. africana*, *Portia fimbriata*, *P. labiata* and *P. schultzi* (Chapter 4, 5 & 8)), there is no evidence that a prior period of two weeks without food has noticeable effects on

prey preferences. Whether these species would become less discriminating after a longer fast needs to be investigated. Also, why the effects of a 2-week fast varied interspecifically needs to be investigated. Nevertheless, it is interesting that this limited study has shown that eight species did alter preference as predicted by OFT.

That these specialized salticids also take standard salticid prey (*e.g.*, flies) besides taking preferred prey (*e.g.*, ants or spiders) appears to be an instance of 'partial preference', a well-known phenomenon also seen in all other studies of prey choice. Pyke (cited in Stephens, 1985) and Gray (1987) have interpreted the existence of partial preference to be a major empirical failing of ODT (Pulliam, 1974; Charnov, 1976). Stephens (1985), however, argued that, because threshold values associated with prey preferences may vary, usually a smooth S-shaped relationship between rates of encounter and proportions of unprofitable prey taken will be observed, instead of a step function. Also, Cheverton *et al.* (1985) argued that finding that a predator has a partial preference is not a failing of OFT but rather a demonstration of our lack of knowledge about causal mechanisms underlying optimal choice. Several explanations of partial preferences have been proposed and discussed by Krebs & McCleery (1984), Stephens & Krebs (1986) and MaNamara & Houston (1987).

The varied reactions to this supposed discrepancy are interesting. Some authors (*e.g.*, Gray, 1987) see here a fatal flaw in ODT, but this interpretation appears to come about because OFT is viewed basically as something that is true or false as a whole. If OFT is viewed as something more like a tool, then whether it is true or false is not entirely a relevant question. More relevant is the question of whether it is useful or not. If OFT is used as a tool, then the 'discrepancy' of partial preferences is recognized as a topic that needs further theoretical or experimental analysis (*e.g.*, see Rechten *et al.*, 1983). From this perspective, OFT has been important as a tool for highlighting what needs more careful study.

Cheverton *et al.* (1985) recognized that ranking of prey should take risk into account. For example, a potential prey may be highly advantageous if only its nutrition value is considered; but it may also be dangerous to the predator,

and the risk the predator must run when hunting this prey may rule out including it in the predator's diet.

Ants, for example, have formidable chemical and mechanical defences that are apparently responsible for how prevalent it is that spiders avoid them, and spiders, being predators, are dangerous prey for each other. Yet, there are myrmicophagic and araneophagic salticids that actually prefer ants and spiders, respectively, to other prey. How did preference for these unusual and dangerous prey evolve in these species? A partial answer appears to be that these salticids have reduced the risk from these dangerous prey by evolving prey-specific prey-capture behaviour. With risk reduced, a factor that probably keeps the profitability ranking of these prey for most salticids low, becomes not so important for the myrmicophagic and araneophagic salticids. However, this can not be the entire explanation.

Possibly another part of the explanation is that myrmicophagic and araneophagic salticids have become metabolically specialized on their respective prey. Evidence for this is currently limited, but the rearing study on *P. fimbriata* (Chapter 9) suggests that this explanation may be true. However, even if we accept metabolic specializations as one reason why the profitability rankings of ants and spiders are higher for the myrmicophagic and araneophagic salticids, respectively, than for most salticids, an important question still remains: why have these salticids evolved this unusual metabolic specialization?

Perhaps, if a salticid has the behaviour needed to be effective at catching particular type of prey (*i.e.*, it has prey-specific capture behaviour), then it can simplify its metabolism. That is, the salticid may become metabolically specialized on this type of prey, but with a trade-off, the trade-off being lesser ability to metabolize other, more 'standard' prey. That is, the possibility that jack-of-all-trades may apply at the level of metabolism should be investigated.

Explaining Queensland *P. fimbriata*'s preference order appears even more challenging. Queensland *P. fimbriata* preferred salticids to web-building spiders and web-building spiders and salticids to insects. This preference order may, in fact, parallel ranking by risk. Cursorial salticids as prey, for *Portia*, may be more dangerous than web-building spiders because they can see well and web-building

spiders must be more dangerous than soft-bodied, non-predatory insects such as flies and moths. If this is so, then Queensland *P. fimbriata*'s preference order, which we expected to match ranking of prey profitability, seems backwards from what we would expect. That is, why progressively more dangerous prey might be progressively more profitable is far from obvious. Perhaps this highlights a particularly interesting challenge for OFT. Alternatively, OFT also may not be the theory (tool) we need, but what are the alternatives?

The optimality framework is primarily a tool investigating ultimate causes of behaviour. Ultimate causes, however, produce a genotype. Proximate causes can potentially act to yield variation in behaviour, behaviour being part of the phenotype. Because of this, the optimality framework may be somewhat restrictive for understanding foraging behaviour, including predatory behaviour and preferences. However, there is a serious lack of alternatives available partly because it has been difficult to develop quantitative non-optimal models that are testable. Predictions are readily derived from optimality models and this is one of the attractions of these models. Also, the logical consequences of natural selection make it difficult to argue why animals might not forage optimally within the boundaries set by constraints (Myers, 1983). That is, OFT is cast within the framework of natural selection theory and ultimate causation (Mayr, 1983) and predictions of optimality seem to follow in a straight-forward way from an appreciation of natural selection. In other words, OFT has the advantage of being built up from first principles of selection theory. Any alternative theory that ignores these first principles is unlikely to be satisfactory to the majority of modern biologists. The best prospect for the future probably lies in continuing efforts to improve OFT as a tool for investigating challenging examples from real animals such as the myrmicophagic and araneophagic salticids.

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